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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. VIII January, 1923 No. 1

THE HEAD-CAPSULE OF COLEOPTERA

WITH TWENTY-SIX PLATES

BY

FENNER SATTERTHWAITE STICKNEY

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Editorial Committee

Stephen Alfred Forbes
William Trelease
Henry Baldwin Ward

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TABLE OF CONTENTS

VOLUME VIII

NUMBERS		PAGES
1.	The head-capsule of Coleoptera. By F. S. Stickney. With 26 plates....	1–104
2.	Comparative studies on certain features of Nematodes and their significance. By D. C. Hetherington. With 4 plates.....	105–166
3.	Parasitic fungi from British Guiana and Trinidad. By F. L. Stevens. With 19 plates.....	167–242
4.	The external Morphology and Postembryology of Noctuid Larvae. By L. B. Ripley. With 8 plates.....	243–344

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Editorial Committee

Stephen Alfred Forbes William Trelease

Henry Baldwin Ward

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THE HEAD-CAPSULE OF COLEOPTERA

WITH TWENTY-SIX PLATES

BY

FENNER SATTERTHWAITE STICKNEY

Contributions from the
Entomological Laboratories of the University of Illinois
No. 71

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ENTOMOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1921

TABLE OF CONTENTS

Introduction 7
Acknowledgments 9
Materials 10
Head-capsule 16
- Epicranial suture 17
- Vertex 20
- Occipital suture 21
- Occiput 21
- Compound eyes 22
- Oculata 22
- Supratentorina 22
- Ocelli 23
- Antennaria 23
- Antacoria 23
- Antacava 23
- Pretentorina 23
- Front 24
- Clypeus 25
- Postclypeus 25
- Clypealia 25
- Mandibularia 26
- Preclypeus 26
- Labrum 26
- Occipital foramen 27
- Submentum 27
- Metatentorina 28
- Cervix 29
- Cervical sclerites 29
- Odontoidea 30
- Postgena 30
- Gula 32
- Epicranium 34
- Paracoila 34
- Postcoila 34
- Precoila 34
- Tentorium 35
- Pretentorium 36
- Metatentorium 37
- Corpotentorium 37
- Laminatentorium 38
- Supratentorium 39

Some Phylogenetic Considerations 40
Summary 48
Bibliography 50

INTRODUCTION

LeConte and Horn published in 1883 a classification of the Coleoptera that has stood the wear of time remarkably well. Since then, however, a number of new classifications have been proposed: Lameere (1900 and 1903), Ganglbauer (1892-1904), Handlirsch (1906-1908), Kolbe (1901, 1908, and 1911), Sharp (1909), and Gahan (1911), all of which differ more or less seriously in one way or another, and show, for one thing, the need of further comparative morphological data, which is, of course, indispensable to the building of any thorough classification. Leng's recent catalogue (1920) also emphasizes this need.

A review of the literature seems to show but few studies based on the comparative morphology of a comprehensive series of coleopterous families. A number of European workers have published comparative studies of the wings of Coleoptera, the most recent being by d'Orchymont (1920). Sharp and Muir (1912) and Muir (1918) have published the results of their investigations on the male genital tube in Coleoptera. Various internal structures have been discussed from time to time by a number of workers. Narrower in scope is the work of d'Orchymont (1916) on the classification of the Hydrophiloidea, based on a study of both the adult and the larva. Hyslop (1917), Böving and Champlain (1920), Craighead (1920), and Gage (1920) have published papers on the comparative morphology of various families, based on a study of the larvae. There are probably other comparative papers more or less extensive in scope, but I have not been able to find any such literature based on a study of the head-capsule, though Crampton (1917, 1920, and 1921) has included the discussion of the coleopterous head in papers not limited to a single order. The comparative morphology of the head-capsule of some other orders, however, has been investigated: Peterson (1915) on the Thysanoptera, Peterson (1916) on the Diptera, Yuasa (1920) on the Orthoptera, and Hoke (1923) on the Plecoptera. These simply draw attention to the need of such an investigation of the head-capsule of Coleoptera.

With the broader vision in mind of a more satisfactory and natural classification of the Coleoptera, the following study on the comparative morphology of the head-capsule is offered. This study does not aim by any means to exhaust the subject. There have been too few species investigated in each family to justify the making of any sweeping statements. This study can simply point out characteristic conditions of structures as found in the different species of the families studied, revealing,

therefore, inharmonies, and perhaps suggesting improvements on the present arrangement of the classification.

In order to reach a correct estimate of the degree of specialization of the various parts of the head-capsule, an hypothetical type, representing a supposed primitive condition, has been constructed. The structure of this hypothetical type is based on the structure of the head-capsule of generalized insects and of generalized adult and larval Coleoptera. Each structure has been treated separately, starting from the hypothetical type. The submentum has been included in this study because of its bearing on certain developmental processes. All statements made refer to the species listed under "materials" only. The material studied was soaked in a 10% solution of potassium hydroxide until clarified, then washed in distilled water to remove the hydroxide, and preserved in 70% alcohol. All dissections were made under a binocular microscope in 70% alcohol in Syracuse watch-glasses.

ACKNOWLEDGMENTS

This study was pursued under the supervision of Professor Alex. D. MacGillivray, to whom I am under the deepest obligations for all that his supervision has meant to me in the way of helpful suggestions and real inspiration. I must further thank him for permission to use his unpublished morphological nomenclature. I am also greatly indebted to Professor S. A. Forbes for suggestions and for furnishing a large number of species from the collections of the Illinois State Natural History Survey and from the collections of the University of Illinois. I am further greatly indebted to Professor H. F. Wickham of the Iowa State University, who supplied me with a considerable number of species belonging to rare families; to Messrs. E. A. Schwarz and H. S. Barber, and the authorities of the United States National Museum for representatives of twelve very rare families from the collections of the Museum; to Mr. W. S. Blatchley of Indianapolis for many very rare species; to Dr. Edwin C. Van Dyke of the University of California for a specimen of a species of Othnius; and to Professor Henry C. Fall for a specimen of Hydroscapha. Of the many courtesies that Dr. Chas. P. Alexander of the Illinois State Natural History Survey has shown me I am duly appreciative. Finally, to Mrs. Elizabeth Stickney, who has helped me greatly in the preparation of the drawings, I am under deep obligations.

MATERIALS

An effort has been made to make this study as comprehensive as possible, including not only a wide series of families, but also a representation of the different subgroups within the families. Of the eighty-one families, exclusive of the Strepsiptera, listed by LeConte and Horn, representatives of all are embraced in this study. Leng in his recent catalogue lists one hundred and nine families. Of these one hundred and five have been studied and figured, representing one hundred and forty-six species. The families in Leng's catalog not included in this study are Telegeusidae with one species, Cerophytidae with two species, Murmidiidae with five species, and Monoedidae with one species. The fundamental structure of the head is, except in a few cases, practically similar for the two sexes. The sex has, therefore, been disregarded, except in the case of the brenthid, *Eupsalis minuta*, the female of which has a long slender snout, as contrasted with the large broad snout of the male. The latter has been figured.

A number of attempts were made to arrange the figures in a linear series leading from the generalized to the specialized forms. All attempts proved unsatisfactory. No matter what structure or condition of a structure was used, the structure showed itself to be unstable within narrow limits, and therefore could not be relied upon to illustrate a definite line of development. However, the meagre results obtained in trying to arrange the drawings in a linear series emphasized an important fact: that the various families of Coleoptera and even the subgroups within the families, have developed along many lines. For this study, the arrangement finally decided on, including the species, is that adopted by Leng. This arrangement will be valuable, in so far as the head-capsule is concerned, in showing the need for further morphological work towards the improvement of our classification of the Coleoptera. Owing to the number of drawings presented in this study it was deemed more practical to omit detailed descriptions. The salient features, only, of the various structures are discussed. The following list is arranged according to Leng's catalog, and includes only those species figured:—

COLEOPTERA

SUBORDER ADEPHAGA

CARABOIDEA.

1. Cicindelidae.

Megacephalini.—Tetracha carolina (Figs. 2, 150, 297, 444).

Cicindelini.—Cicindela formosa (Figs. 3, 151, 298, 445).

2. Carabidae.
   Carabinae.—Calosoma calidum (Figs. 4, 152, 299, 446).
   Harpalinae.—Harpalus erraticus (Figs. 5, 23, 24, 153, 300, 447).
3. Amphizoidae.—Amphizoa lecontei (Figs. 6, 154, 301, 448).
4. Omophronidae.—Omophron americanum (Figs. 7, 155, 302, 449).
5. Haliplidae.—Peltodytes 12-punctatus (Figs. 8, 156, 303, 450).
6. Dytiscidae.—Cybister fimbriolatus (Figs. 9, 157, 304, 451).

GYRINOIDEA.

7. Gyrinidae.—Dineutes americanus (Figs. 10, 158, 305, 452).

SUBORDER POLYPHAGA

HYDROPHILOIDEA.

8. Hydrophilidae.
   Hydraeninae.—Hydraena marginicollis (Figs. 11, 159, 306, 453).
   Hydroscaphinae.—Hydroscapha natans (Figs. 12, 160, 307, 454).
   Hydrophilinae.—Hydrous triangularis (Figs. 13, 161, 308, 455).
   Hydrophilus obtusatus (Figs. 14, 162, 309, 456).

SILPHOIDEA.

9. Platypsyllidae.—Platypsyllus castoris (Figs. 15, 163, 310, 457).
10. Brathinidae.—Brathinus nitidus (Figs. 16, 164, 311, 458).
11. Leptinidae.—Leptinus testaceus (Figs. 17, 165, 312, 459).
12. Silphidae.—Necrophorus carolinus (Figs. 18, 166, 313, 460).
13. Clambidae.—Clambus puberulus (Figs. 19, 167, 314, 461).
14. Scydmaenidae.—Connophron fossiger (Figs. 20, 168, 315, 462).
15. Orthoperidae.—Molamba lunata (Figs. 21, 169, 316).

STAPHYLINOIDEA.

16. Staphylinidae.
   Steninae.—Stenus flavicornis (Figs. 22, 170, 317, 463).
   Paederinae.—Gastrolobium bicolor (Figs. 25, 171, 318, 464).
   Staphylininae.—Creophilus villosus (Figs. 26, 172, 319, 465).
   Tachyporinae.—Tachinus fimbriatus (Figs. 27, 173, 320, 466).
   Aleocharinae.—Aleochara lata (Figs. 28, 174, 321, 467).
17. Pselaphidae.—Pilopius lacustris (Figs. 29, 175, 322, 468).
18. Clavigeridae.—Fustiger fuchsi (Figs. 30, 176, 323).
19. Ptilidae.—Limulodes paradoxus (Figs. 31, 177, 324, 469).
20. Sphaeriidae.—Sphaerius politus (Figs. 32, 178, 325, 470).
21. Scaphidiidae.—Scaphidium quadriguttatum (Figs. 33, 179, 326, 471).
22. Sphaeritidae.—Sphaerites glabratus (Figs. 34, 180, 327, 472).
23. Histeridae.—Hister memnonius (Figs. 35, 181, 328, 473).

CANTHAROIDEA.

24. Lycidae.—Calopteron terminale (Figs. 36, 182, 329, 474).
25. Lampyridae.—Photinus pyralis (Figs. 37, 183, 330, 475).
26. Phengodidae.—Phengodes plumosa (Figs. 38, 184, 331, 476).

27. Cantharidae.
    Chauliognathini.—Chauliognathus pennsylvanicus (Figs. 39, 185, 186, 332, 477).
    Cantharini.—Cantharis bilineatus (Fig. 187).
28. Melyridae.—Collops nigriceps (Figs. 40, 188, 333, 478).
29. Cleridae.—Trichodes nutalli (Figs. 41, 189, 334, 479).
30. Corynetidae.—Necrobia rufipes (Figs. 42, 190, 335, 480).

LYMEXYLOIDEA.

31. Lymexylidae.—Hylecoetus lugubris (Figs. 43, 191, 336, 481).
32. Micromalthidae.—Micromalthus debilis (Figs. 44, 192, 337).

CUPESOIDEA.

33. Cupesidae.—Cupes concolor (Figs. 45, 193, 338, 482).

MORDELLOIDEA.

34. Cephaloidae.—Cephaloon lepturides (Figs. 46, 194, 339, 483).
35. Oedemeridae.—Nacerda melanura (Figs. 47, 195, 340, 484).
36. Mordellidae.—Tomoxia bidentata (Figs. 48, 196, 341, 485).
37. Rhipiphoridae.—Macrosiagon dimidiatum (Figs. 49, 197, 342, 486).
38. Meloidae.—Epicauta marginata (Figs. 50, 198, 343, 487).
39. Eurystethidae.—Eurystethus debilis (Figs. 51, 199, 344, 488).
40. Othniidae.—Othnius sp. (Figs. 52, 200, 345, 489).
41. Pythidae.—Pytho planus (Figs. 53, 201, 346, 490).
42. Pyrochroidae.—Neopyrochroa flabellata (Figs. 54, 202, 347, 491).
43. Pedilidae.—Macratria murina (Figs. 55, 203, 348, 492).
44. Anthicidae.—Notoxus anchora (Figs. 56, 204, 349, 493).
45. Euglenidae.—Zonantes fasciatus (Figs. 57, 205, 350, 494).

ELATEROIDEA.

46. Cebrionidae.—Cebrio bicolor (Figs. 58, 206, 351, 495).
47. Plastoceridae.—Euthysanius lautus (Figs. 59, 207, 352, 496).
48. Rhipiceridae.—Sandalus niger (Figs. 60, 208, 353, 497).
49. Elateridae.—Alaus oculatus (Figs. 61, 209, 354, 498).
50. Eucnemidae.—Isorhipis ruficornis (Figs. 62, 210, 355, 499).
51. Throscidae.—Throscus chevrolati (Figs. 63, 211, 356, 500).
52. Buprestidae.—Chalcophora virginiensis (Figs. 64, 212, 357, 501).

DRYOPOIDEA.

53. Psephenidae.—Psephenus lecontei (Figs. 65, 213, 358, 502).
54. Dryopidae.—Helichus striatus (Figs. 66, 214, 359, 503).
55. Elmidae.—Stenelmis sinuata (Figs. 67, 215, 360, 504).
56. Heteroceridae.—Heterocerus undatus (Figs. 68, 216, 361, 505).
57. Georyssidae.—Georyssus californicus (Figs. 69, 217, 362, 506).

DASCILLOIDEA.

58. Dascillidae.—Eurypogon niger (Figs. 70, 218, 363, 507).
59. Eucinetidae.—Eucinetus morio (Figs. 71, 219, 364, 508).

60. Cyphonidae.—Cyphon ruficollis (Figs. 72, 220, 365, 509).
61. Chelonariidae.—Chelonarium errans (Figs. 73, 221, 366, 510).

Byrrhoidea.

62. Dermestidae.—Dermestes lardarius (Figs. 74, 222, 367, 511).
63. Byrrhidae.—Byrrhus americanus (Figs. 75, 223, 368, 512).
64. Nosodendridae.—Nosodendron unicolor (Figs. 76, 224, 369, 513).

Rhysodoidea.

65. Rhysodidae.—Rhysodes americanus (Figs. 77, 225, 370, 514).

Cucujoidea.

66. Ostomidae.—Tenebroides sinuatus (Figs. 78, 226, 371, 515).
67. Nitidulidae.
    Nitidulinae.—Phenolia grossa (Figs. 79, 227, 372, 516).
    Cryptarchinae.—Glischrochilus fasciatus (Figs. 80, 228, 373, 517).
68. Rhizophagidae.—Rhizophagus bipunctatus (Figs. 81, 229, 374, 518).
69. Monotomidae.—Phyconomus marinus (Figs. 82, 230, 375, 519).
70. Cucujidae.
    Cucujini.—Cucujus clavipes (Figs. 83, 231, 376, 520).
    Hemipeplini.—Hemipeplus marginipennis (Figs. 84, 232, 377, 521).
71. Erotylidae.
    Langurinae.—Languria mozardi (Figs. 85, 233, 378, 522).
    Erotylinae.—Megalodacne fasciata (Figs. 86, 234, 379, 523).
72. Derodontidae.—Derodontus maculatus (Figs. 87, 235, 380, 524).
73. Cryptophagidae.—Anchicera ephippiata (Figs. 88, 236, 381, 525).
74. Byturidae.—Byturus unicolor (Figs. 89, 237, 382, 526).
75. Mycetophagidae.—Mycetophagus punctatus (Figs. 90, 238, 383, 527).
76. Colydiidae.
    Bothriderini.—Bothrideres geminatus (Figs. 91, 239, 384, 528).
    Cerylonini.—Philothermus glabriculus (Figs. 92, 240, 385, 529).
77. Lathrideridae.—Melanophthalma cavicollis (Figs. 93, 241, 386, 530).
78. Mycetaeidae.—Phymaphora pulchella (Figs. 94, 242, 387, 531).
79. Endomychidae.—Endomychus biguttatus (Figs. 95, 243, 388, 532).
80. Phalacridae.—Phalacrus politus (Figs. 96, 244, 389, 533).
81. Coccinellidae.—Hippodamia convergens (Figs. 97, 245, 390, 534).
    Adalia bipunctata (Figs. 98, 246, 391, 535).

Tenebrionoidea.

82. Alliculidae.—Pseudocistela brevis (Figs. 99, 247, 392, 536).
83. Tenebrionidae.—Alobates pennsylvanica (Figs. 100, 248, 393, 537).
    Tenebrio molitor (Figs. 101, 249, 394, 538).
    Boros unicolor (Figs. 102, 250, 395, 539).
84. Lagriidae.—Arthromacra aenea (Figs. 103, 251, 396, 540).
85. Monommidae.—Hyporphagus sp. (Figs. 104, 252, 397, 541).
86. Melandryidae.—Penthe obliquata (Figs. 105, 253, 398, 542).

87. Ptinidae.—Ptinus brunneus (Figs. 106, 254, 399, 543).
88. Anobiidae.—Sitodrepa panicea (Figs. 107, 255, 400, 544).
89. Bostrichidae.—Bostrichus bicornis (Figs. 108, 256, 401, 545).
90. Lyctidae.—Lyctus planicollis (Figs. 109, 257, 402, 546).
91. Sphindidae.—Sphindus americanus (Figs. 110, 258, 403, 547).
92. Cisidae.—Plesiocis cribrum (Figs. 111, 259, 404, 548).

SCARABAEOIDEA.

93. Scarabaeidae.
    Aphodiinae.—Aphodius fimetarius (Figs. 112, 260, 405, 549).
    Melolonthinae.—Dichelonyx elongata (Figs. 113, 261, 406, 550).
    Rutelinae.—Pelidnota punctata (Figs. 114, 262, 407, 551).
    Dynastinae.—Strategus julianus (Figs. 115, 263, 408, 552).
    Cetoniinae.—Osmoderma eremicola (Figs. 116, 264, 409, 553).
94. Trogidae.—Trox suberosus (Figs. 117, 265, 410, 554).
95. Lucanidae.—Pseudolucanus capreolus (Figs. 118, 266, 411, 555).
96. Passalidae.—Passalus cornutus (Figs. 119, 267, 412, 413, 556).

CERAMBYCOIDEA.

97. Cerambycidae.
    Prioninae.
      Parandrini.—Parandra brunnea (Figs. 120, 268, 414, 557).
      Prionini.—Derobrachus brunneus (Figs. 121, 269, 415, 558).
    Cerambycinae.
      Spondylini.—Spondylis buprestoides (Figs. 122, 270, 416, 559).
      Clytini.—Glycobius speciosus (Figs. 123, 271, 417, 560).
    Lamiinae.—Tetraopes tetrophthalmus (Figs. 124, 272, 418, 561).
98. Chrysomelidae.
    Donaciinae.—Donacia piscatrix (Figs. 125, 273, 419, 562).
    Orsodacninae.—Syneta ferruginea (Figs. 126, 274, 420, 563).
    Criocerinae.—Criocerus asparagi (Figs. 127, 275, 421, 564).
    Cryptocephalinae.—Cryptocephalus quadruplex (Figs. 128, 276, 422, 565).
    Eumolpinae.—Chrysochus auratus (Figs. 129, 277, 423, 566).
    Chrysomelinae.—Leptinotarsa decemlineata (Figs. 130, 278, 424, 567).
    Galerucinae.—Diabrotica 12-punctata (Figs. 131, 279, 425, 568).
    Halticinae.—Blepharida rhois (Figs. 132, 280, 426, 569).
    Hispinae.—Anoplitis gracilis (Figs. 133, 281, 427, 570).
    Cassidinae.—Chelymorpha argus (Figs. 134, 282, 428, 571).
99. Mylabridae.—Pachymerus gleditsiae (Figs. 135, 283, 429, 572).

BRENTOIDEA.

100. Brentidae.—Eupsalis minuta (Figs. 136, 284, 430, 573).

CURCULIONOIDEA.

101. Belidae.—Ithycerus noveboracensis (Figs. 137, 285, 431, 574).

102. Platystomidae.—Eurymycter fasciatus (Figs. 138, 286, 432, 575).
103. Curculionidae.
Rhinomacerinae.—Rhinomacer pilosus (Figs. 139, 287, 433, 576).
Rhynchitinae.—Rhynchites bicolor (Figs. 140, 288, 434, 577).
Attelabinae.—Attelabus analis (Figs. 141, 289, 435, 578).
Otiorhynchinae.—Epicaerus imbricatus (Figs. 142, 290, 436, 579).
Curculioninae.—Lixus fimbriolatus (Figs. 143, 291, 437, 580).
Thecesterninae.—Thecesternus humeralis (Figs. 144, 292, 438, 581).
Calendrinae.—Sphenophorus aequalis (Figs. 145, 293, 439, 582).

SCOLYTOIDEA.

104. Platypodidae.—Platypus flavicornis (Figs. 146, 294, 440, 583).
105. Scolytidae.
Scolytinae.—Scolytus quadrispinosus (Figs. 147, 295, 441, 584).
Hylesininae.—Dendroctonus valens (Figs. 148, 296, 442, 585).

HEAD-CAPSULE

There exists a distinct homogeneity in the general character of the structure of the head-capsule of Coleoptera. Its uniform strong chitinization is typical. So is the spacious area occupied by the mouth-parts, producing a relatively broad cephalic end. Especially characteristic is the wide space between the occipital foramen and the submentum. Then, there is that indescribable similarity of structure, even between groups widely separated, that can best be appreciated from a thorough knowledge of the morphology. As an illustration, there is little superficial resemblance between Harpalus (Figs. 5 and 153) and Phalacrus (Figs. 96 and 244), either in external or in internal morphology. Their distinct differences are merely due to two divergent lines of development. The structures of the dorsal surface of Phalacrus have become highly specialized, whereas those of Harpalus are relatively generalized. On the other hand, on the ventral surface the metatentorina has remained in a relatively primitive condition in Phalacrus, whereas in Harpalus its position is highly specialized. The internal structures of Phalacrus are rudimentary or lacking, while in Harpalus they are in a well developed primitive state. Considering the degree of generalization of each species, there can hardly be any question that Harpalus is the more generalized. The above comparative description simply illustrates roughly the problems of complexity of development that are encountered. The two distinctive kinds of development as shown above for Harpalus and Phalacrus, that of specialization of the dorsal surface and that of separate specialization of the ventral surface, do not in the least necessarily parallel one another in the Coleoptera. Indeed, these two lines of development are predominantly divergent. In the majority of species, the development is trending towards the obliteration of sutures and consequent consolidation of sclerites, and towards the development of a compactness of form of the sclerites that do not consolidate. The general trend towards a cephalization of migratory structures is a part of this process, too, as well as the development of a stronger chitinization of the head-capsule as a whole. The entire phenomenon appears to be for purposes of strengthening the head. Besides Phalacrus typical examples are Tenebrioides (Fig. 78), Glischrochilus (Fig. 80), Megalodacne (Fig. 86), and all the Scarabaeoidea. On the other hand these processes have lagged behind on the ventral surface in Phalacrus and others. It is true that the hypothetical type (Fig. 149) shows a marked cephalization of the submentum, with obliteration of

sutures resulting from this migration. Yet the predominant condition of the heads studied shows only a certain degree of removal from the primitive type. Stronger chitinization has probably kept pace with the cephalization of the dorsal surface, as well as the growing compactness of such a structure as the submentum. But the very significant structure of the ventral surface, the metatentorina, only shows a certain degree of removal from the primitive condition in most of the heads.

Developmental processes such as are discussed above can be best worked out through a comparative study of a large series of forms. In fact the determination of the homologies of some structures entering into these developmental processes, as for example the various changes in the epicranial suture, and the determination of the nature and line of development of the area between the occipital foramen and the submentum, would probably be most difficult without this comparative study. The chief value of this study lies in all probability in the determination of homologies, to the end of understanding the lines of development present. The homology existing between the various structures of the head-capsule of Coleoptera and other orders of insects, particularly the generalized orders, seems to work out satisfactorily. From such an homology the hypothetical type was constructed without much difficulty. In general appearance the head is oblong and rather flattened dorso-ventrally. Such a form is fairly characteristic of generalized insects and of the more generalized Coleoptera. The mouth may be considered as directed cephalad. Such a direction is representative of the vast majority of the heads, and for purpose of convenience, at least, the following discussion considers the head as extending cephalad. Some possible exceptions in which the head appears to be directed ventrad are found in Calopteron (Fig. 329), Macrosiagon (Fig. 342), Isorhipis (Fig. 355), Throscus (Fig. 356), Byrrhus (Fig. 368), and a few others. It should not be forgotten, however, that in primitive insects the mouth is directed ventrad, and the occipital foramen is on one side instead of at the opposite end.

The line of closure of the head in the embryo is represented by the epicranial suture. The complete epicranial suture is typical of generalized insects. Where it is present in Coleoptera, this denotes a generalized condition. The primitive form of the epicranial suture is that of a deep inverted Y, with the cephalic ends of the arms near the lateral border of the labrum. The hypothetical head is represented as having a complete epicranial suture. The epicranial stem extends to a transverse line drawn through the middle of the compound eyes. Branching here the epicranial arms continue to the margin of the head cephalad of the compound eyes. A complete epicranial suture is not of general occurrence in the Coleoptera. It is practically complete in Hydrous (Fig. 13) and Hydrophilus (Fig. 14),

very distinct and sharply invaginated in both, particularly so in the former, and characteristic in form. Each arm reaches the margin of the head almost immediately cephalad of a compound eye, and the arms are not as generalized in position as they are in Epicauta (Fig. 50), where they are quite distinct. The only other occurrence of a complete epicranial suture is in Chelymorpha (Fig. 134). Here the arms meet the stem farther caudad than in the other genera named. The arms in this last genus are distinctly curved, as contrasted with the more or less straight arms in the above mentioned genera.

The epicranial arms or some portion of them are present in all Coleoptera, except possibly in Calopteron (Fig. 36) and Photinus (Fig. 37). One or more species of every superfamily of the Adephaga and Polyphaga, except the Elateroidea, Byrrhoidea, Rhysodoidea, and Rhynchophora, have the arms complete. In the Caraboidea they are prominent as nearly straight sutures across the head, as in Tetracha (Fig. 2), Cicindela (Fig. 3), Calosoma (Fig. 4), and Harpalus (Fig. 5). Their most generalized condition in the Adephaga is found in Omophron (Fig. 7) in which they extend from the meson at a sharp angle. Representative species of other superfamilies that have the arms complete are: Necrophorus (Fig. 18), Tachinus (Fig. 27), Chauliognathus (Fig. 39), Cupes (Fig. 45), Cephaloon (Fig. 46), Notoxus (Fig. 56), Heterocerus (Fig. 68), Eucinetus (Fig. 71), Mycetophagus (Fig. 90), Tenebrio (Fig. 101), Bostrichus (Fig. 108), Aphodius (Fig. 112), and nearly all the Cerambycoidea. Species having parts of the epicranial stem preserved are not very common. In Omophron (Fig. 7), Tachinus (Fig. 27), Penthe (Fig. 105), and a number of the Cerambycoidea, parts of the cephalic end can be identified; in Omophron (Fig. 7), Phengodes (Fig. 38), Cupes (Fig. 45), Sitodrepa (Fig. 107), Blepharida (Fig. 132), and a number of the Rhynchophora, parts of the caudal end are present. Chalcophora (Fig. 64) and Tetraopes (Fig. 124) are peculiar in possessing practically all of the stem but little of the arms. The arms in Chalcophora are as short as in any other species studied. Parts of the arms are present in every degree of length from nearly meeting on the meson, as in Nosodendron (Fig. 76), to almost complete disappearance as in Chalcophora (Fig. 357) and Rhysodes (Fig. 370). They also show varying degrees of disappearance and invagination, from the deep distinct invaginations of such forms as Dineutes (Fig. 10), Necrophorus (Fig. 18), Tachinus (Fig. 27), Heterocerus (Fig. 68), and Arthromacra (Fig. 103), to the faint or slender and shallow or not at all invaginated sutures characteristic of the Scarabaeoidea.

The character of the invagination associated with the epicranial arms is not as simple as may be thought. In Harpalus (Figs. 5 and 24), the epicranial arms extend from the meson along the edge of the invagination to the pretentorinae, from which they extend to the bottom of the invagi-

nation, curve laterad, and continue to the margin of the head. The course of the epicranial arms can be better understood from Omophron (Fig. 7), a related genus, which has retained the cephalic portion of the epicranial stem. The line of the invagination appears to be and often is considered to be simply the clypeal suture. If a specimen of Harpalus is soaked for a long time in potassium hydroxide the invagination can be opened and the various structures in this region studied advantageously. The invagination when opened (Fig. 24) will be seen to assume a deep wide wedge-shaped form, extending entirely across the dorsal surface of the head. The pretentorinae are located on the external dorsal surface just caudad of the cephalic margin of the invagination. Although the epicranial arms are not in evidence anywhere between the meson and the pretentorinae, it is assumed that the cephalic marginal ridge must represent them, since the pretentorinae are not only located caudad of the invagination, but the arms are quite distinct, extending from the pretentorinae to the bottom of the invagination, in which they then curve laterad and continue to the margin of the head. From a cross-section (Fig. 23) it will be seen that the pretentorium expands cephalad in characteristic form from the pretentorina along an epicranial arm to the bottom of the invagination. In Calosoma (Fig. 4) the same condition of this region is found as in Harpalus. In Omophron (Fig. 7) the epicranial arms are distinct between the pretentorinae, extending from the meson along the cephalic border of the invagination. From Figure 24 it will be observed that the cephalic border of the invagination in Harpalus is along the imaginary line of the fronto-clypeal suture. This border may represent the cephalic limit of the front. The invagination, then, in Harpalus and Calosoma includes the entire front. The line of the invagination instead of being solely a part of the epicranial suture is in fact compound in nature, representing the approximation of the caudal borders of the front and postclypeus, and that part of it between the pretentorinae may be termed the "clypofrons." Laterad of the pretentorinae to the margin of the head the line of the invagination is readily seen to be an approximation of a part of the vertex with the caudal border of the postclypeus and cannot be included in the clypofrons. Due to the more primitive position of the epicranial arms in Omophron the invagination in this genus contains only a part of the front, hence the line of the invagination between the pretentorinae is simple in nature. In Tachinus (Fig. 27) the epicranial stem extends distinctly into the invagination, the arms continuing in the same to the margin of the head. As should be expected, the pretentorinae are within the invagination. The line of the invagination in Tachinus is then of a different character from that of either Harpalus or Omophron. In Tachinus, it has nothing whatever to do with the epicranial suture nor with any other suture, being throughout the approximation of parts of the external dorsal surface of

the vertex and the front. It is obvious from the above discussion of three types of the invagination associated with the epicranial arms that the dorsal surface of the head-capsule in Coleoptera must be studied most carefully before a correct interpretation of the parts can be made. This is most true in the case of any invagination that may be present. The latter may not be readily observed when the head-wall is strongly and darkly chitinized, necessitating treatment of such specimens before the parts can be clearly made out. In Dermestes (Fig. 74), and perhaps others, all external trace of the line of the invagination may be lost. In such cases a true understanding of the parts can only be gained from an examination of the ental surface of the head. But in specialized forms the ental indication of the invagination may also be effaced.

The epicranial suture can always be located from the determination of the position of the pretentorina. The latter is always closely associated with the epicranial suture, being present either in or just off of the suture, in which case the pretentorina resembles a sort of pocket. There is usually little difficulty experienced in locating the suture. The cephalic ends of the arms are the most persistent parts of it, being present when the remainder of the suture cannot be identified. Interesting examples are found in most Rhynchophora, where the remnants of the epicranial arms are represented by short furrows located at the cephalic end of the snout. The epicranial arms are typically structures of the dorsal aspect, but with the shifting and modification of other parts of the head may be confined to the lateral aspect, as in Helichus (Fig. 359), Adalia (Fig. 391), or to the ventral aspect, as in Cybister (Fig. 157), Hydrous (Fig. 161) and Phalacrus (Fig. 244). From the preceding discussion of the epicranial suture it is seen that what appears superficially to be this suture may not be so. It is a difficult problem to understand the kind and amount of change that may have taken place. In a number of the Rhynchophora, for instance, what appears to be the epicranial stem (Figs. 146 and 147) may be only invaginations, for in these same species are lateral invaginations that are quite similar in form to the so-appearing epicranial stem. The epicranial stem seems to the writer to hold the strongest claims, so these invaginations are considered as such. So, in other instances, where a structure appears to be more definitely the epicranial suture than anything else, it is so interpreted.

That part of the head-capsule not embraced by the three primary sclerites cephalad of the epicranial arms, the occiput, and the postgena, constitutes the vertex. Its extent is determined by the form and size of the three above mentioned areas. For instance, in those species with much reduced epicranial arms, as in Creophilus (Fig. 26), Adalia (Fig. 98), and Phalacrus (Fig. 96), the extent of the vertex is correspondingly increased. In the Rhynchophora, as represented by such species as Lixus

(Fig. 143) and Sphenophorus (Fig. 145) it is very extensive, including practically all of the snout of the dorsal and lateral surfaces. The area on the lateral surfaces of the head, cephalad of the compound eyes, between the latter and the epicranial suture, is the gena, a part of the vertex. The limits of the gena are not definite. The prominent ridge in many genera, dorso-mesad of each gena and antacoria, is the so called frontal ridge, that extends in the general direction from the epicranial arms to the mesal margin of the compound eyes. The frontal ridge is prominent in Harpalus (Fig. 5), Necrophorus (Fig. 18), Trichodes (Fig. 41), Neopyrochroa (Fig. 54), Dermestes (Fig. 74), and many others.

In generalized insects the occipital suture is confined to the ventral or caudal aspect, beginning near the lateral margin of the postcoila and extending around the caudal or dorsal margin of the occipital foramen. In the Coleoptera this suture arises laterad of the postcoila, extends cephalad for a considerable distance, then curves abruptly laterad, extending onto the dorsal aspect of the head, where it joins the suture of the other side of the meson. The genus Cicindela (Figs. 3, 151, and 298) possesses the most generalized condition of this suture found in the Coleoptera. The cephalic end of the suture is modified into a ridge. This ridge is considered a later development, and is not shown in the hypothetical type. It unquestionably represents a part of the occipital suture, and can be identified in practically all the Coleoptera, as in such widely separated groups as Molamba (Fig. 168), Nacerda (Fig. 195) and Byturus (Fig. 237). The occipital suture separates the vertex from the occiput and the postgena. Only the Caraboidea seem to possess with certainty an unmodified occipital suture. In Cicindela (Fig. 3) it is complete and nearly so in Tetracha (Figs. 2, 150, and 297), but very faint in great part. In Calosoma (Fig. 152) the unmodified suture begins farther caudad and is more distinct. In Omophron (Fig. 302), two short, characteristically curved, lateral ridges no doubt represent remnants of the occipital suture. The ridge across the lateral aspect in Peltodytes (Fig. 303) may also represent this suture. In Cybister (Fig. 157) it is probably represented by the crescent-shaped suture on the ventral aspect. Ridges and furrows appearing in the same general location in other species, such as Aleochara (Fig. 321), Throscus (Fig. 356), Cyphon (Fig. 365), and Aphodius (Fig. 405), may possibly be homologized as occipital sutures. In most cases these ridges seem to be merely to mark the limits to which the head is telescoped in the prothorax.

In those species possessing an occipital suture the occiput is recognized as a distinct area. It includes the region between the occipital foramen and the occipital suture as far as the postgena, appearing as a sort of broad band across the dorsal aspect, divided by the epicranial stem and indistinguishably fused on the lateral aspect with the postgenae. Examples

of a well marked occiput are present in Tetracha (Fig. 2), Cicindela (Fig. 3), Calosoma (Fig. 4), and Harpalus (Fig. 5). In Omophron (Fig. 302) the occipital suture is so short that the limits of the occiput cannot be definitely determined. In those species not possessing a recognizable unmodified portion of the occipital suture, the limits of the occiput can only be judged accordingly. Even in generalized insects the occiput is nearly always fused with the postgenae, and is so represented in the hypothetical type.

There is a great similarity in the form and location of the compound eyes. The general form is oval. They are located near the middle of the lateral margin of the head. Such a form and location is given in the hypothetical type. There are a number of interesting variations in form from the normal type. Dineutes (Fig. 305) and Tetraopes (Fig. 124) have four complete eyes. This phenomenon is produced by a projection of a part of the vertex into the eye that in time completely separates the two halves. The line of closure between the projection and the opposite side is indicated by a distinct line—the exoculata. The beginning of such a projection is shown in Cephaloon (Fig. 46), Epicauta (Fig. 50) and many others. In Pseudocistela (Fig. 99) and Osmoderma (Fig. 116) the projection extends more than half-way across the eye. In Throscus (Fig. 63) the projection nearly separates the two halves. The eyes of Peltodytes (Fig. 8), Photinus (Fig. 37) and Stenus (Fig. 22) are very large. Unusual forms of the eyes are found in Hypophagus (Fig. 104), where they are very long and narrow nearly meeting on the dorso-meson; in Cryptocephalus (Fig. 128), where they are prominent, crescent-shaped, and extend well caudad on the dorsal surface; and in Aphodius (Fig. 112), where they are relatively small and square-like. The eyes of Limulodes (Fig. 324) are transparent and almost invisible; those of Leptinus (Fig. 312) are completely wanting.

The oculata is present only on the inside periphery of the eye as a broad ring-like shelf. It is considered of little importance in this study. Its general size is indicated by the dotted area within the eyes of Cicindela (Fig. 298), Dineutes (Fig. 305), Passalus (Fig. 412), and a few others. In forms with divided eyes the two sides of an oculata are pressed together, forming an exoculata.

The supratentorinae represent the point of attachment on the head-capsule of the supratentoria. They are not thought to be primary invaginations, and may probably represent no more than depressions. In the Coleoptera the supratentorinae are not prominent, as the pretentorinae and metatentorinae often are. They are situated on the dorsal surface of the vertex. Their presence is not general, occurring commonly only in the Staphylinoidea. Outside of this superfamily the supratentorinae are found only in Phyconomus (Fig. 82) and Philothermus (Fig. 92). The

supratentoria are usually attached to the inner membrane of the body-wall, but unless an actual mark of their presence is indicated on the external surface the supratentorinae are not considered as present. In generalized insects the latter are generally present. Their presence in the Coleoptera should indicate a primitive state.

In all the Coleoptera examined, no indication of any ocelli has been observed.

In generalized insects there is a ring-like sclerite surrounding the periphery of each antacoria. In Coleoptera this sclerite is present, but it is distinguished from the head-capsule by a ridge only. On most heads it is considerably reduced in size, about all that can be seen of it externally being its projection, the antacoila, upon which the scape of the antenna articulates. On the other hand, in Sandalus (Fig. 353), Derobrachus (Fig. 120), Tetraopes (Fig. 124), Leptinotarsa (Fig. 130), and Anoplitis (Fig. 133), the antennaria is quite prominent. The most generalized position of the antennaria is considered to be on the gena cephalad of the eye, notwithstanding that in generalized insects the antennariae are quite frequently found distinctly between the eyes. Embryology, however, shows that the antennae are postoral in origin. Furthermore, in coleopterous larvae each antennaria is located cephalad of the ocellarae. Such a position in coleopterous adults should denote the more generalized condition. The antennaria is very unstable in position. There is hardly a superfamily in which it does not appear in both the generalized position and elsewhere. In the Scarabaeoidea and Cerambycoidea, though the position of the antennaria varies within certain limits, yet it shows a characteristic location. In the former it is either on the lateral or ventral aspects, while in the latter it occurs only on the dorsal aspect. In no other large groups does the antennaria appear so constant in position. In Calopteron (Fig. 36) and Phengodes (Fig. 38) it is exceptionally large; in Dineutes (Fig. 305) and Alobates (Fig. 392) it is exceptionally small.

The membrane attaching the antenna to the head-capsule is the antacoria. In removing the antennae the antacoria is torn, and as it plays no significant part in this study no attempt was made to represent it in every case. The antacoria varies in size depending upon the size and shape of the scape. It is indicated in a number of figures by the stippled area: Omophron (Fig. 7), Necrophorus (Fig. 313), Calopteron (Fig. 36), Phengodes (Fig. 38), and Chauliognathus (Fig. 332).

The depression in the vertex, usually in the gena, within which the antennaria and antacoria are situated is the antacava. It is always present, so far as is known, and is developed into a deep socket in Dineutes (Fig. 305), Connophron (Fig. 315), Scolytus (Fig. 441), and Dendroctonus (Fig. 442).

The points of invagination of the pretentoria on the head-capsule are the pretentorinae. They are always located along the epicranial suture

in the Coleoptera. In generalized insects and the more generalized Coleoptera, they are situated on the lateral margin of the head. They are, therefore, represented in this position on the hypothetical type. The pretentorinae have been identified in every species studied except possibly Calopteron (Fig. 36) and Photinus. In the latter they are represented by depressions caudad of the eyes. Their position along the epicranial suture varies greatly. In widely separated groups they may be primitively located, as illustrated in such diverse forms as Omophron (Fig. 7), Necrophorus (Fig. 18), Scaphidium (Fig. 33), Chauliognathus (Fig. 39), Cephaloon (Fig. 46), Nacerda (Fig. 47), Alaus (Fig. 61), Phyconomus (Fig. 82), and Glycobius (Fig. 123). The position of the pretentorina evidently cannot possess any important significance in every instance, yet its position may be characteristic sometimes. In the Scarabaeoidea it is never on the dorsal surface; in the Cerambycoidea it is always on the dorsal surface. In this respect, the pretentorinae and the antennariae behave similarly. As a matter of fact, they are usually associated together, but there are some striking exceptions. The antennariae of Macrosiagon (Fig. 49) are located well caudad of the cephalic margin of the eyes, while the pretentorinae are situated at the ventro-lateral margin of the head (Fig. 342). The opposite condition is found in Phenolia (Fig. 79). The antennariae in the vast majority of cases are caudad of the pretentorinae.

The pretentorinae are the great landmarks of the head-capsule. On their location the determination of the presence and position of the epicranial suture is often dependent, and, consequently, the homologies of large areas of the head-capsule. A case in point is that of the Rhynchophora, in which the pretentorinae are located near the cephalic end of the snout, on the dorso-lateral margin. The epicranial suture is reduced to the very short cephalic ends of the epicranial arms, and though we cannot, therefore, indicate with precision the cephalic limits of the vertex, its approximate limits can be judged, which would show the vertex to occupy nearly all the dorsal and lateral aspects of the snout.

The sclerite embraced by the epicranial arms is the front. In the hypothetical type (Fig. 1) its caudal and lateral limits are the epicranial arms. Its cephalic limit is indistinguishable, since the front is fused with the postclypeus. The approximate line of fusion is indicated by a dotted line. There is no external indication in any head of a fronto-clypeal suture. The size of the front depends upon the position and direction of the epicranial arms. In those species possessing the inverted Y type of arms, the front assumes considerable proportions, but where the arms have been forced into a more or less straight line across the head, the invagination associated with the epicranial arms includes practically the entire front. As mentioned previously, the epicranial arms extend in this manner across the head in a wide series of families. The front must hence assume this

form. In just as wide a series of families, the epicranial arms are in process of disappearing. In such cases, the caudal limits of the front can only be judged approximately. In great reduction of the arms, as represented by Phalacrus (Fig. 96) and Macrosiagon (Fig. 49), the vertex, the front and the postclypeus are indistinguishably fused into one area.

In all species the clypeus is divided into two distinct sclerites, the postclypeus and the preclypeus. This condition is not present so far as I know in the more generalized insects such as the Orthoptera and Plecoptera. In some Neuroptera, however, the preclypeus is a large characteristic sclerite, quite similar to what has been designated as the preclypeus in the Coleoptera. It may possibly represent the extraordinary development and differentiation of the labracoria, but its size, shape and form would militate against such an assumption. It seems much easier to believe that this area is a true sclerite, and in this discussion it will be so considered.

The broad cephalic part of the area between the epicranial arms in the hypothetical type (Fig. 1) represents the postclypeus. In generalized Coleoptera it is of considerable size if the dorsal surface has retained a generalized form. The shape, form, and size of the postclypeus is correlated with the position and extent of the epicranial arms, which has already been discussed. In highly specialized forms like the Scarabaeoidea (Figs. 114, 115, and 116), the postclypeus may be even more extensive. Among the Staphylinidae, the postclypeus may be very large in Tachinus (Fig. 27) and Aleochara (Fig. 28), and very small in Creophilus (Fig. 26). In Chalcophora (Fig. 357) the cephalic end of the vertex is located on the ventral aspect of the head, and the postclypeus is reduced to hardly more than a line. Among the Cerambycoidea the postclypeus is generally very large. In the Rhynchophora it is quite reduced in size.

The caudo-lateral projection or lobe of the postclypeus is the clypealia. In Orthoptera and Plecoptera the clypealia is not separated from the remainder of the postclypeus. In the larvae of Corydalis it is a prominent distinct sclerite. The clypealia in the Coleoptera is often separated from the postclypeus proper by a distinct furrow or suture. It is quite loosely attached to the postclypeus in the Cicindelidae (Figs. 297 and 298), the Carabidae (Figs. 299 and 300), many of the Cerambycoidea (Figs. 419 and 424), and others. Difficulty is often experienced in removing the mandibles from the head without detaching the clypealia. The close resemblance between the Neuroptera and the Coleoptera in other respects would lead one to believe that this similar structure in the two orders must be homologous. The presence of this furrow in the Coleoptera is wide-spread, as a glance at the figures will show. It can probably show little significance as an indication of primitiveness. It must, though, have been present in the primitive Coleoptera, and is hence shown in the hypothetical type.

In most of the Orthoptera a small triangular area is present, extending from the precoila to the cephalic end of the occipital suture. This sclerite is known as the mandibularia. No such area has been located in the Coleoptera.

The dorsal surface of the larvae of Corydalis is very generalized. On this surface there is a prominent submembranous sclerite between the postclypeus and the labrum, the preclypeus. Such a sclerite, very similar in size, form, texture, and position, is present in Tachinus (Fig. 27), Arthromacra (Fig. 103), Trichodes (Fig. 41), and Glycobius (Fig. 123). This sclerite is considered the preclypeus. Figure 23 is a longitudinal section of the dorsal aspect of the head of Harpalus, and shows the characteristic position of the preclypeus. It is always present in the Coleoptera, though often considerably reduced in size. The preclypeus is always membranous except in Photinus (Fig. 37), where it is chitinized and the labrum is membranous. Besides the forms mentioned above, the preclypeus is large and prominent in Necrophorus (Fig. 18), Connophron (Fig. 20), Macratria (Fig. 55), Philothermus (Fig. 92), Hippodamia (Fig. 97), and many others. Very frequently the cephalic end of the postclypeus is infolded, thus carrying the preclypeus and the labrum with it. In such cases the preclypeus cannot be seen from the dorsal aspect. The preclypeus, no matter how deeply it is infolded, is, except in a few cases, sharply differentiated from the postclypeus and the labrum. In Glischrochilus (Fig. 373) and Chauliognathus (Fig. 332) the postclypeus and the labrum were in such close approximation that the preclypeus could not be observed until the two above mentioned sclerites were separated, and this was possible only after long soaking in potassium hydroxide. In most of the Rhynchophora, due to the fusion or absence of the labrum, the preclypeus could not be identified. The preclypeus, however, was prominent in Attelabus (Fig. 141), and somewhat reduced in Epicaerus (Fig. 290).

The broad prominent sclerite attached to the cephalic end of the clypeus in generalized insects is the labrum. In Coleoptera possessing other generalized structures, the labrum is typically of the same general form. The labrum is shown in the hypothetical type. In position the hypothetical labrum should be, with the preclypeus, in accordance with their condition in generalized insects, on the same general level with the remainder of the dorsal surface. The generalized form and position of the labrum is present in every superfamily except the Elateroidea, Dryopoidea, Rhysodoidea, Scarabaeoidea, and the Rhynchophora, in which the postclypeus has been infolded, thus forcing the labrum onto the ventral aspect. All the superfamilies containing species with the labrum generalized, contain about as many with it in various degrees of specialization, as to form, size, texture and position. The labrum in Con-

nophron (Fig. 20), Photinus (Fig. 37), Othnius (Fig. 52), Chelonarium (Fig. 73), Eurymycter (Fig. 138), and others, is large and membranous. The labrum of Aphodius (Fig. 260) is large but very thin and delicate. The labrum of Scolytus (Fig. 295) and Dendroctonus (Fig. 296) is probably membranous. In the latter, a significant looking slightly chitinized structure is located in the membrane within the mouth that may represent the labrum. In Thecesternus (Fig. 292) there is a membranous area closely joined to the postclypeus that probably represents the labrum. In Eupsalis (Fig. 284), Lixus (Fig. 291), Sphenophorus (Fig. 293), and Rhynchites (Fig. 288), there is an area within the mouth, bounded by furrows, that may be the labrum. Such are particularly suggestive in view of the fact that in the same location and lying flat against the postclypeus a very thin but a relatively large and well chitinized labrum was found in Epicaerus (Fig. 290) and Attelabus (Fig. 289). The labrum in Isorhipis (Fig. 210), Nosodendron (Fig. 224), Phyconomus (Fig. 230), and Derobrachus (Fig. 269) is considerably reduced in size. It is present in every species, except possibly the rhynchophorous genera named above, where it is always said to be wanting.

The prominent opening in the caudal part of the head is known as the occipital foramen. It is generally very large, but in some species, such as Connophron (Fig. 168), Cephaloon (Fig. 194), and Macratria (Fig. 203) is reduced in dimensions, due to the constriction of the caudal end of the head. In Calopteron (Fig. 182), Photinus (Fig. 183), Alaus (Fig. 209), and Tetraopes (Fig. 272), the occipital foramen is extraordinarily large.

In order to understand clearly the developmental processes that take place on the ventral surface, it is necessary to consider a sclerite, belonging to the mouth-parts, the submentum. In generalized insects the submentum is not only adjacent to but is one of the covering parts of the occipital foramen. Such a position is not found in the Coleoptera. Here, it is always located cephalad of the occipital foramen, with a distinct area between the two. In the vast majority of heads this area is very wide. It is considered as having been present in primitive forms, and is shown on the hypothetical type. The submentum in generalized insects is a large quadrangular movable plate. Many genera of Coleoptera show a similar size, form, and mobility, as in Leptinus (Fig. 165), Necrophorus (Fig. 166), Stenus (Fig. 170), Nacerda (Fig. 195), Neopyrochroa (Fig. 202), Alaus (Fig. 209), Heterocerus (Fig. 216), Cyphon (Fig. 220) and Byrrhus (Fig. 223). In these three characters, and the additional one of position in respect to the paracoila, which in generalized insects is normally found beneath the submentum, that of the Adephaga seems to be the most primitive. The innumerable sizes and forms assumed by this structure throughout the entire series of families can best be judged by glancing at the figures. It is extraordinarily large in Rhysodes (Fig. 225).

The invaginations on the external surface of the head-capsule of the metatentoria are the metatentorinae. In the Orthoptera the metatentorinae are located along the cephalo-lateral or ventro-lateral border of the occipital foramen as invaginations between the maxillariae and the postgenae. They are not in any way associated with the submentum in generalized insects or in the Coleoptera. The same relative position of the metatentorinae is maintained in the Plecoptera. In a number of Coleoptera, as in Helichus (Fig. 214), Stenelmis (Fig. 215), Heterocerus (Fig. 216), and even in the platystomid, Eurymycter (Fig. 286), this same generalized position of the metatentorinae is found. In a number of Coleoptera the metatentorinae are situated considerably cephalad of the occipital foramen. The question might be raised as to whether the metatentorinae that are so located could possibly be more generalized in position than those situated adjacent to the occipital foramen? In every instance in which the metatentorinae are located cephalad of the occipital foramen, a suture connects the metatentorinae with the occipital foramen. In only a few cases does the suture extend much farther cephalad than the metatentorinae. This suture in the vast majority of heads studied does not extend cephalad. It is readily seen how the metatentorinae might be drawn cephalad and as a result a suture be formed marking their line of migration. In such a process one would naturally not expect to find a suture located cephalad of the metatentorinae, and in the cases in which the suture does extend so it is easy to understand that the force of the cephalic pull might have been communicated to this region, producing in consequence a suture or invagination. Due to the shape of the head, it is most difficult to believe that the metatentorinae could be drawn caudad, and if they were so drawn, it would seem that in this process there would be formed a suture cephalad of the metatentorinae, marking the line of migration. In this discussion the generalized position of the metatentorinae will be considered as that of its generalized position in more primitive insects, at or near the occipital foramen.

In the development of the coleopterous head the metatentorinae have shown a tendency to migrate cephalad. The cephalic migration of the metatentorinae and the ventral migration of the pretentorinae and other structures, were no doubt due to the same force, the result being a closer approximation of parts, which naturally supplied increased firmness to the head's mechanics of operation. The Dryopoidea show the most generalized position of the metatentorinae. Genera of this superfamily have been mentioned above. The Elateroidea probably possess the next most generalized metatentorinae, such as in Sandalus (Fig. 208) and Alaus (Fig. 209). The Cucujoidea show the metatentorinae just a little removed from the occipital foramen, as in Megalodacne (Fig. 234), Anchicera (Fig. 236), Philothermus (Fig. 240), and others. In the genera of other super-

families, as Nosodendron (Fig. 224), Anoplitis (Fig. 236) and Tetraopes (Fig. 272), almost the same degree of primitiveness is shown. The large superfamily Mordelloidea show the metatentorinae to have migrated to about half the distance between the occipital foramen and the submentum. This condition is fairly consistent throughout the group. In the Bostrichoidea, the Scarabaeoidea, and the Cerambycoidea, the metatentorinae show considerable variation in position. This is shown by a comparison of their position in Bostrichus (Fig. 256) and Sphindus (Fig. 258). In the families to which Tetracha (Fig. 150), Calosoma (Fig. 152), Cybister (Fig. 157), Dineutes (Fig. 158), Necrophorus (Fig. 166), and Glycobius (Fig. 271) belong, the metatentorinae have advanced very far cephalad, near to the submentum. In Photinus (Fig. 183) and Chauliognathus (Fig. 185) they are located on or quite near the paracoila.

There is a narrow plate surrounding the lateral and caudal margins of the occipital foramen in some generalized insects, between which and the postgenae the metatentorinae are invaginated. This plate has disappeared in the Coleoptera.

The structure connecting the head-capsule with the prothorax is called the cervix. It is normally composed of membrane, and a number of cervical sclerites. The size of the cervix depends upon the size of the occipital foramen, and the degree of mobility of the head. In the Lampyroidea and some other forms the cervix is very large. The cervix in Rhysodes is composed of tough fibrous membrane, quite different in structure from the normal cervix. In nearly all of the Rhynchophora the cervix is heavily supported by strong tendons attached at its cephalic end. These tendons take care of the added strain on the cervix due to the elongation of the snout. There are more or less small cervical tendons appearing occasionally throughout the whole series of families studied. In Molamba (Fig. 21) the cervix is invaginated within the prothorax, doubling upon itself. The cervix in Bostrichus (Figs. 256 and 401) doubles back upon the head-capsule, which is produced into a round projection.

The most prominent and persistent cervical sclerites are the pleural cervical sclerites, the cervepisternum and the cervepimeron. The former is usually the larger of the two, and articulates at its cephalic end either against an odontoidea or simply against the undifferentiated area surrounded by the occipital foramen. The latter usually extends in a different direction from the former, and articulates at its cephalic end with the cervepisternum and at its caudal end with the prothorax. In Cantharis (Fig. 187), Macratria (Fig. 348), Psephenus (Fig. 358) and others, there is a single large sclerite present. In the Adephaga, in Leptinus (Fig. 312), Hyporphagus (Fig. 397), Pseudocistela (Fig. 392), and many others, there is a single small subcircular sclerite present. Both of these types probably

represent the cervepisternum. In a very large number of genera cervical sclerites are always wanting. They are poorly or not at all developed in the Cerambycoidea. None of the Rhynchophora studied possess a cervical sclerite except Eurymycter (Fig. 452), in which it is very small. The ventral cervical sclerite is the cervisternum. Hister (Fig. 181), Nacerda (Fig. 195), Cucujus (Fig. 251), and a few others, possess two small cervisterna, while Tomoxia (Fig. 196) possesses a long narrow one. The cervisternum is on the whole of infrequent occurrence. The dorsal cervical sclerite is called the cervinotum. It occurs even less frequently than the cervisternum. Hydrous (Fig. 15) possesses a subquadrangular distinctly chitinized cervinotum. In Aleochara (Fig. 28) the cervinotum is divided into two distinct lightly chitinized subtriangular sclerites. Two much larger square-like sclerites are situated caudad of these. All of the Hydrophilidae and Scarabaeidae possess setaceous caudo-lateral sclerites, which do not seem to be present in the other genera studied.

Owing to the strong chitinization of the head and the close fit of the head in the prothorax, there is little need for a special process or projection on the head for the articulation of the cervepisternum. Such a process is called an odontoidea. Some of the species in which it does occur are Scaphidium (Fig. 179), Endomychus (Fig. 219), Cyphon (Fig. 220), Byrrhus (Fig. 223), Nosodendron (Fig. 224), and Arthromacra (Fig. 251). The latter genus, it is interesting to note, possesses no cervepisternum.

That part of the head-capsule on the caudal surface, mesad of the occipital suture and ventrad of each occiput, in generalized orthopterous insects is a postgena. The occiput is considered as extending to near the middle of the dorso-ventral length of the occipital foramen, thus limiting the dorsal extent of the postgenae. The latter are widely separated from each other by the occipital foramen. The lateral parts of the large submentum distinctly cover the mesal parts of the postgenae. In the Coleoptera the occipital suture separates this region from the remainder of the head-capsule, as in generalized insects, and the occiput is also indistinguishably fused with the postgenae. But the postgenae, instead of being widely separated and their mesal parts being covered by the lateral parts of the submentum are directly connected by the broad area located between the occipital foramen and the submentum (Fig. 149); and the submentum is attached to the mesal portion of the cephalic margin of the postgenae. This area is indistinguishably fused with and undifferentiated from the postgenae in the hypothetical and the more generalized types of ventral surface.

In generalized insects the submentum is joined to the cervix by the undifferentiated part of the cervix, the cervacoria. In the cephalic migration of the submentum, a part or all of the cervacoria must have been drawn in behind. The postgenae alone bordered the lateral margins of

the submentum and the cervacoria. A possible line of development may have been the chitinization of the cervacoria and the disappearance of the sutures separating it from the postgenae. The broad area between the occipital foramen and the submentum would in such a case be a modification of part or all of the cervacoria. It is much easier to believe, instead, that because of the membranous condition of the cervacoria, no strong resistance was offered to an approach of the mesal margins of the chitinous postgenae, which would migrate thus to serve as a firm foundational support for the submentum, as well as to strengthen the solidity of the head-capsule, as a whole. The mesal margins would in time approach so close as to press the two sides of the cervacoria into a line. Fusion of the mesal margins of the postgenae would finally take place, and the cervacoria would be divided into two parts. One part would be attached to the submentum entirely separated from that portion of the cervacoria bordering the occipital foramen, and would be finally reduced to a suture. The other part of the cervacoria would remain as a portion of the cervix. Whether the mesal margins of the postgenae would approach the meson as broad surfaces, or as narrow ones and later elongate, it would be difficult to state with certainty, though the latter would probably happen. In the primitive coleopterous head it is not unlikely that the head was much shorter, and that the area between the occipital foramen and the submentum was correspondingly shorter, so that there would not be the necessity for a broad fusion of the mesal margin of the postgenae. So far as observed there has been retained in no coleopterous head any marks of the line of fusion of the postgenae.

Abundant evidence is found for the conclusion that the broad area between the occipital foramen and the submentum must be a part of the postgenae. A similar condition as in the Coleoptera is present in many families of insects. In many Hymenoptera the mesal margins of the postgenae are fused between the occipital foramen and the articulation of the labium. That this is the true interpretation of this structure is shown by the fact that there is often a suture on the meson showing the line of fusion, and is further substantiated by the fact that this area bears on its ventral margin the paracondylae. In all cyclorrhaphous and orthorrhaphous Diptera the area ventrad of the occipital foramen is a continuous chitinized piece similar to that found in the Coleoptera, and is derived from the fusion of the mesal margins of the postgenae.

It may be well to add here that the expression "cephalic migration," as applied to the changed location of such a structure as the submentum, may be only relatively correct in its suggestion. Very probably the occipital foramen in Coleoptera has migrated dorsad, at least it has assumed this typical position. Such a migration in itself would produce an elongation of the ventral surface, with a consequent production of the broad area

between the occipital foramen and the submentum. Whether the force exerted on the head was directed more towards the cephalization of the submentum or towards the dorsalization of the occipital foramen it would be hard to say. The condition resulting would be in either case approximately the same. For purposes of convenience and simplicity of language, the expression "cephalic migration" is used in this discussion.

This broad area between the occipital foramen and the submentum is sometimes designated as the gula. Usually, though, the term gula is used to indicate a sclerite, on the meson of the ventral aspect, separated from the remainder of the head-capsule by distinct subparallel sutures, the gular sutures. The term gula cannot satisfactorily be applied to both an indefinite region and a distinct sclerite. The gula is considered in the latter sense in this discussion. For the present the area between the occipital foramen and the submentum will simply be designated as the mesal parts of the postgenae.

The cephalic end of a postgena is usually modified into a rather flat area sloping towards the meson, upon which is situated a paracoila and a postcoila. This flat area is distinguished from the remainder of the postgena by a distinct ridge, which usually extends in a deep curve from near the lateral margin of a postcoila to near the caudo-lateral margin of the submentum. Sometimes this ridge is directed towards the occipital foramen, as in Leptinus (Fig. 165), Cantharis (Fig. 187), Macrosiagon (Fig. 197), Isorhipis (Fig. 210), Psephenus (Fig. 213), Helichus (Fig. 214), and others. Attention has already been called to the fact that the cephalic portion of this ridge represents the cephalic end of the occipital suture. This modified part is reduced in size or indistinguishably fused with the remainder of the head, in Photinus (Fig. 183), Eucinetus (Fig. 219), Alobates (Fig. 248), Tenebrio (Fig. 249), Hyporphagus (Fig. 252), most of the Scarabaeoidea, Sphenophorus (Fig. 293), Eupsalis (Fig. 284), and Lixus (Fig. 291).

There seems to be considerable confusion as to what constitutes the gula. Some investigators consider it as simply the central portion of the ventral surface of the head-capsule. Others restrict it to the distinct sclerite appearing on the meson of the ventral surface of certain insects, including the Coleoptera. Since this sclerite is distinctive and characteristic it needs a name. The term gula is quite satisfactory to apply to it. The origin of the gula also rests in considerable confusion. Comstock and Kochi (1902) consider it the sternum of the cervical segment, and to strengthen their argument they cite the situation in Corydalis, in which they state that the sternellum of the cervical segment is retained back of the gula, and they figure it as the small quadrangular sclerite immediately caudad of the gula. They do not mention the very much larger rectangular cervical sclerite caudad of their "sternellum." The larger sclerite is sug-

gestive of the sternellum, and the smaller one would then represent their "sternum." It is generally stated that the gula is derived from the chitinization of the neck membrane or cervix. In the discussion preceding, dealing with the metatentorinae and the postgenae, I have attempted to show the impossibility of such a derivation. In many orders of insects structures on the caudal aspect of the head have been designated as the gula. My interpretation would prevent the recognition of the presence of the gula in any insects other than the Coleoptera, Neuroptera, and Trichoptera.

In some Coleoptera there is no gula (Figs. 168, 177, and possibly 286), whereas in others there is a complete gula (Figs. 150, 157, 172, 185, 267, and 296). Between these extreme types there are found in the Coleoptera all gradations of a gula in process of formation (Figs. 156, 187, 210, 245, and 257). Such a range of variation in a structure simply emphasizes the importance of a comparative study of a large series of forms. The question as to which is the more generalized condition, the presence of a complete gula or the absence of one, has been previously discussed, with the verdict in favor of the latter condition. It would then be impossible, other reasons not being considered, for the gula to be the sternum of the cervical segment. The gula is the sclerite formed by the migration of the metatentorinae from the occipital foramen towards the submentum, and must be derived from the postgenae. In this migration of the metatentorinae sutures are produced which are known as the gular sutures. The area between the gular sutures is the gula. It is evident, then, that the presence and extent of the gula depend upon the position of the metatentorinae and the sutures which they produce. The gula is complete in all the Adephaga except Peltodytes (Fig. 156), in the Silphidae, the Staphylinidae, the Sphaeriidae, the first four families of the Canthroidea, and the Scarabaeidae except Pseudolucanus (Fig. 266). Isolated examples in other families of a complete gula are Scaphidium (Fig. 179), Helichus (Fig. 214), Cyphon (Fig. 220), Byrrhus (Fig. 223), and Leptinotarsa (Fig. 278). The gular sutures nearly meet in Gastrolobium (Fig. 171) and Creophilus (Fig. 172), and are entirely confluent in Necrophorus (Fig. 166), Scaphidium (Fig. 179), Hister (Fig. 181), Phengodes (Fig. 184), Chauliognathus (Fig. 185), and in all the Rhynchophora except Eurymycter (Fig. 286) and Rhinomacer (Fig. 287) in which genera the gular sutures are very widely separated. In Rhinomacer the gular sutures extend nearly half the distance to the submentum. The gula in cases of confluency of the middle portion of the gular sutures on the meson is simply invaginated. The gula is complete but extremely short in Calopteron (Fig. 182) and Photinus (Fig. 183). The cephalic ends of the gular sutures meet on the meson near the occipital foramen in Philothermus (Fig. 240) and Anoplitis (Fig. 280). The gula is partially membranous in Nosodendron (Fig. 224),

Sitodrepa (Fig. 255), and Plesiocis (Fig. 259). Part of it is deeply invaginated transversely in Scaphidium (Fig. 179), Chauliognathus (Fig. 185), Helichus (Fig. 214), Stenelmis (Fig. 215), and others.

Most of the sclerites of the head-capsule are so closely united in some Coleoptera as to appear as a single piece. Strauss-Durckheim (1828) so regarded this region in the head-capsule of the May-beetle, and named it the epicranium. Used in the sense of indicating a closely united area, the term seems satisfactory and may often prove convenient. It can then be only a relative term, including at times no more than the paired sclerites of the head, when the epicranial suture is well developed. Occasionally, the preclypeus and the labrum are closely joined to the head-capsule. In such cases, the epicranium would embrace these structures, also.

The small rather concave projections at the caudo-mesal margins of the postgenae against which the maxillae articulate are the paracoilae. They are usually easily identified, as in Molamba (Fig. 169), Pytho (Fig. 201), Heterocerus (Fig. 216), and Phymaphora (Fig. 242). They are usually chitinized, but are membranous in a considerable number of genera. The paracoilae are insignificant in size in Gastrolobium (Fig. 171), all of the Elateroidea, Pseudocistela (Fig. 247), and Tenebrio (Fig. 249). In generalized insects the paracoilae are situated beneath the submentum. They are found in a similar position in the Adephaga (Figs. 150, 152, 154, 157, and 158), in Hydrous (Fig. 161), and a few others. They are also always located on the postgenae in generalized insects. This position is of great importance in determining the identity of the postgenae in specialized insects.

At the cephalic end of a postgena is always found a distinct crescent-shaped acetabulum—the postcoila, against which the postartis of the mandible articulates. Throughout the genera the postcoilae exhibit some degree of difference in exact position upon the postgenae, in size, and in degree of shallowness. Their form and position are indicated in Calosoma (Fig. 152), Sphaerius (Fig. 178), Notoxus (Fig. 204), and Derobrachus (Fig. 269). In generalized insects the postcoilae are also always located on the postgenae, and their position is of equal importance with that of the paracoilae in determining the identity of the postgenae.

The rounded condyle on the ventral surface of each clypealia, against which the preartis of the mandible articulates is the precoila. It is usually crescent-shaped, but sometimes, as in Peltodytes (Fig. 156), Cybister (Fig. 157), Creophilus (Fig. 172), Endomychus (Fig. 243), Dichelonyx (Fig. 261), and others, the form is spherical. The precoilae are large in Macrosiagon (Fig. 197), Epicauta (Fig. 198), Isorhipis (Fig. 210), Chauliognathus (Fig. 185), Bostrichus (Fig. 256), and others, and small in Dineutes (Fig. 158), Photinus (Fig. 183), Helichus (Fig. 214), Derodontus (Fig. 235), and particularly so in Psephenus (Fig. 213). The precoilae can

readily be recognized by their characteristic form. Since they are always located on the caudo-lateral lobe of the postclypeus, or the clypealia of certain insects, they are a great aid in determining the limits of the postclypeus.

The endoskeleton of the head is known as the tentorium. It is composed of two anterior and two posterior areas or projections, and their various modifications. The anterior arms arise from the pretentorinae, and are known as the pretentoria. The posterior arms arise from the metatentorinae, and are known as the metatentoria. In generalized insects one end of the pretentorium expands along and is continuous with the epicranial suture. Each extends in a caudo-mesal direction, and narrows for a short distance, then expands along its mesal margin until a fusion is formed with the pretentorium of the other side, producing the cephalic bridge, or laminatentorium. The pretentoria separate and then fuse again farther caudad with each metatentorium. The metatentoria extend cephalo-mesad a very short distance, their mesal margins expand and completely fuse on the meson, producing the caudal bridge or corpotentorium. The fusion of the pretentoria and the metatentoria is supposed to take place along the cephalic margin of the corpotentorium. The dorsal projections arising from the lateral margins of the pretentoria and extending toward and attached to the dorsal wall of the head, are the supratentoria. The ring-like plate surrounding the inside periphery of the occipital foramen is indistinguishably fused with and is a part of the metatentoria. The tentoria, as a whole, are distinctly chitinized and well developed. The typical condition of the tentorium in generalized insects is practically duplicated among the Coleoptera. The hypothetical type (Fig. 443) has been constructed with this similarity in mind. The greatest difficulty experienced was in deciding upon the primitive type of laminatentorium, whether it should be represented as complete or incomplete, that is, whether the two sides of the laminatentorium fuse on the meson or not. Many Coleoptera that in other respects are quite generalized do not show a complete laminatentorium, as Tetracha (Fig. 444), Omophron (Fig. 449), Dineutes (Fig. 452), Leptinus (Fig. 459), Tachinus (Fig. 460), and Stenelmis (Fig. 504). The hypothetical laminatentorium is represented as nearly meeting on the meson. At least, such a condition is thought to be not far removed from that which actually existed in the primitive Coleoptera. Limulodes (Fig. 469), Eurystethus (Fig. 488), Pytho (Fig. 490), Philothermus (Fig. 529), Melanophthalmus (Fig. 530), Hyporphagus (Fig. 541), Sphindus (Fig. 547), and others, possess practically no trace of a laminatentorium, but well developed supratentoria. The atter are fairly well developed in Photinus (Fig. 475), Collops (Fig. 478), and Alaus (Fig. 498), but there is neither a laminatentorium nor a corpoentorium present. There is no trace of any one of the three above

mentioned structures in Isorhipis (Fig. 499) and Throscus (Fig. 500). Phalacrus (Fig. 533) and Eurymycter (Fig. 575) possess only the rudiments of the pretentoria and metatentoria. The tentoria of the Cerambycoidea (Figs. 557, 560 and 566) are very delicate and membranous. The pretentoria, the metatentoria, and the corpotentorium are always complete, while the laminatentorium and supratentoria are always either rudimentary or absent except in Pachymerus (Fig. 572) in which the supretentoria are present. Other genera showing completely membranous tentoria are numerous. Among these are Cupes (Fig. 482), Eurystethus (Fig. 488), Rhysodes (Fig. 514), Languria (Fig. 522), and Pseudocistela (Fig. 536).

A generalized condition of the pretentorium, characterized by a strong chitinization as a whole, and possessing a broad flaring cephalic end, is found in the Adephaga (Figs. 449 and 451), Leptinus (Fig. 459), Necrophorus (Fig. 460), the Staphylinidae (Figs. 465 and 467), Georyssus (Fig. 506), Eucinetus (Fig. 508), Dermestes (Fig. 511), and Derodontus (Fig. 524). There are all degrees of gradation present from the most generalized pretentoria to those very delicate membranous ones represented by such forms as Heterocerus (Fig. 505), Endomychus (Fig. 532), Pseudocistela (Fig. 536), Hyporphagus (Fig. 541), the majority of the Cerambycoidea, and the Rhynchophora. A very prevalent type, possessing a distinctly chitinized cephalic end and a membranous caudal portion sharply separated from the former, is represented in Epicauta (Fig. 487), Pytho (Fig. 490), Chalcophora (Fig. 501), Alobates (Fig. 536), Bostrichus (Fig. 545), Diabrotica (Fig. 568), Dendroctonus (Fig. 585) and most of the Scarabaeoidea. Rudimentary pretentoria are found in a number of genera, as Calopteron (Fig. 474), Tenebroides (Fig. 515), Phalacrus (Fig. 533), and perhaps all of the Rhynchophora, except Dendroctonus. The pretentoria of the Rhynchophora are for the most part very delicate and fragile. The difficulty of making a dissection showing the pretentoria intact is intensified by the close packing within the snout of the greatly developed tendons of the mouth-parts and the strongly chitinized pharynx. In no instance, except in Dendroctonus was a pretentorium preserved intact. In Scolytus (Fig. 584), the pretentorium is evidently rudimentary, but in none of the other genera is there a clear indication of such being the case, owing to the presence of frayed ends, suggesting that not all of the pretentorium has been seen. The presence in the Rhynchophora (Figs. 433, 435, 437, 439 and 441) of a suture in the right position for an epicranial suture, an invagination within the suture that suggests the pretentorina, and a projection arising from the invagination, all furnish evidence that this projection is probably the cephalic portion of the pretentorium. The pretentorium of Passalus (Fig. 413) is extraordinarily developed. The cephalic part extends as a slender bar dorso-caudad, nearly half way to the occipital foramen, then bends suddenly and extends as a huge

straight arm toward the corpotentorium. The tremendous development of the caudal part is due to the need of a strong support for the dorsal surface, which bears a prominent horn used in fighting.

The form and size of the metatentorium is quite decidedly indicated by the position of the metatentorinae. Those genera possessing primitive metatentorinae are very apt to possess the primitive type of metatentorium, one that is short and simple, as Limulodes (Fig. 469), Sphaerius (Fig. 470), Anchicera (Fig. 535), Philothermus (Fig. 529), Melanophthalmus (Fig. 530), and Sphindus (Fig. 547). It is significant to note that all of these genera are very small in size. The cephalic migration of the metatentorinae is due to a similar movement of the metatentoria. In those genera in which the metatentorinae have migrated from their primitive position near the occipital foramen, the metatentoria are found more or less deeply invaginated along the gular sutures, the sutures being the products of these invaginations. In most genera the metatentoria advance but little or not at all farther cephalad than the metatentorinae, but there are some exceptions, in which the metatentoria taper gradually, as in Helichus (Fig. 503), Cyphon (Fig. 509), Lyctus (Fig. 546), and all of the Scarabaeoidea, except Pseudolucanus (Fig. 555). In those genera in which the gular sutures are confluent on the meson, the gula itself is simply invaginated, becoming a part of the metatentorium. The same type of development has taken place in Necrophorus (Fig. 460), Scaphidium (Fig. 471), Hister (Fig. 473), Phengodes (Fig. 470), Chauliognathus (Fig. 477), and Georyssus (Fig. 506), as in the Rhynchophora. In Necrophorus, Phengodes, Chauliognathus, Eupsalis (Fig. 573) and Thecesternus (Fig. 581), the line of fusion of the invaginations of the two sides has disappeared. In Chauliognathus the invagination is greatly reduced, and in Phengodes nothing remains but a mere line. These two latter genera seem to show a greater specialization of the gular region than any other genera studied. A correspondingly deeper invagination of the ring-like plate surrounding the inside periphery of the occipital foramen has occurred with that of the gula. The whole phenomenon appears to be due to an especially strong cephalic pull on the metatentoria. This can be readily understood in the case of the Rhynchophora, in which the elongation of the snout would encourage this result. A second force may play a part here, that of the narrowing of the snout, which might assist in the enfoldment of the gula.

A large number of genera, scattered throughout the series of families, possess prominent projections along the mesal margins of the metatentoria, caudad of the corpotentorium, as those of Cybister (Fig. 451), Necrobia (Fig. 480), Glischrochilus (Fig. 517), Phyconomus (Fig. 519), and Boros (Fig. 539). Some of these projections have distinct tendons attached to them, as in Scaphidium (Fig. 471), Parandra (Fig. 557), Derobrachus (Fig. 558), Donacia (Fig. 562), and Criocerus (Fig. 564). Prominent

lateral projections are present in Lyctus (Fig. 546), Osmoderma (Fig. 553), Parandra, Glycobius (Fig. 560), Rhynchites (Fig. 577), Epicaerus (Fig. 579), and Thecesternus (Fig. 581). Passalus (Fig. 556) is peculiar in the possession of a large well chitinized secondary bridge arising from the mesal margin of the metatentoria.

Owing to the simplicity of form of a structure like the corpotentorium, but little change is indicated in it through most of the genera. The hypothetical type shows this structure to be a rather narrow simple band (Fig. 443). Such is fairly characteristic of the vast majority of forms. The corpotentorium is sometimes very broad, as in Ptinus (Fig. 543), Bostrichus (Fig. 545), Parandra (Fig. 557), Derobrachus (Fig. 558), Glycobius (Fig. 560), and Eupsalis (Fig. 573). In contrast are many that are quite slender and arched, as Dineutes (Fig. 452), Stenus (Fig. 463), Hister (Fig. 473), Georyssus (Fig. 506), and Mycetophagus (Fig. 527). The form of these latter has evidently resulted from the narrowing of the space between the metatentoria. An exceptionally large number of genera have only a rudimentary corpotentorium, or none at all, as in all of the Lampyroidea except Trichodes (Fig. 479) and Necrobia (Fig. 480), Epicauta (Fig. 487), Macrosiagon (Fig. 486), all of the Elateroidea, Psephenus (Fig. 502), Rhysodes (Fig. 514), Phalacrus (Fig. 533), Hippodamia (Fig. 534), and Arthromacra (Fig. 540). The reasons for the loss of the corpotentorium are not always evident, though in most cases, either the arms of the tentoria have expanded and approximately met on the meson, as in Rhysodes and Plesiocis (Fig. 548), or the arms are directed towards the meson and meet there, as in Connophron (Fig. 462) and all of the Elateroidea, or the pharynx rests snugly between the tentorial arms, as is so perfectly found in Chauliognathus (Fig. 477), where the pharynx is wedged so tightly between them that the whole seems like one piece, all of which conditions supply firmness to the tentorial arms and obviate the necessity for a corpotentorium. Of the Rhynchophora, Eurymycter (Fig. 575), Epicaerus (Fig. 579), Platypus (Fig. 583) and Lixus (Fig. 580) possess no corpotentorium. Scolytus (Fig. 584) possesses a very rudimentary one. The disappearance of the corpotentorium can best be explained in the case of the Rhynchophora by the fusion of the metatentoria into one solid plate that needs no added support. The corpotentorium of most of the Cerambycoidea is a delicate membranous structure. A common modification of the corpotenterium is the mesal projections on its cephalic border, as in Tachinus (Fig. 460), Cephaloon (Fig. 483), Tomoxia (Fig. 485), Phenolia (Fig. 510), and Philothermus (Fig. 529).

A structure of the tentorium that shows perhaps a greater variability in form than any other is the laminatentorium, which appears in a great array of shapes and sizes, from the forming of a perfect and broad bridge to total disappearance. When the two sides of the laminatentorium meet

on the meson, the mesal margins of the laminatentorium very frequently are bent ventrad, producing a projection. Examples of this development are seen in Calosoma (Fig. 446), Cybister (Fig. 451), Necrophorus (Fig. 460), Aleochara (Fig. 467), Heterocerus (Fig. 505), Dermestes (Fig. 511), and Endomychus (Fig. 532). Genera that show the laminatentorium as hardly more than touching on the meson are Peltodytes (Fig. 450), Scaphidium (Fig. 471), Neopyrochroa (Fig. 481), Notoxus (Fig. 493), Psephenus (Fig. 502), Cucujus (Fig. 520), Penthe (Fig. 542), and most of the Scarabaeidae. The reduction of the laminatentorium takes place so gradually that it is hard to tell when it has completely disappeared. There seems to be no indication of it in Limulodes (Fig. 469), Collops (Fig. 478), Pseudocistela (Fig. 536), Hyporphagus (Fig. 541), Sphindus (Fig. 547), and others. In Tomoxia (Fig. 485), Pytho (Fig. 490), Alaus (Fig. 498), Tharops (Fig. 499), Throscus (Fig. 500), and others, there is no laminatentorium. The pretentorial arms curve towards the meson and serve a similar purpose. The laminatentorium of Tachinus (Fig. 460) and Epicauta (Fig. 487) is in the form of a lobe. That of Psephenus (Fig. 502), Dichelonyx (Fig. 550), and Pelidnota (Fig. 551), possesses two long sharp cephalic projections.

Arising from the dorsal surface of each pretentorium cephalad of the laminatentorium and usually extending towards the dorsal surface of the head is a projection of variable form, the supratentorium. Its generalized condition would show a rather distinctly chitinized structure, with an expanded ventral end that gradually narrows, then expands flat-like against the ental surface of the head-wall. This kind of structure is found in a very large number of genera, as all of the Adephaga except Peltodytes (Fig. 450), the Hydrophilidae, Leptinus (Fig. 459), all of the Staphylinoidea except Aleochara (Fig. 467), and Hister (Fig. 473), Pytho (Fig. 490), Nosodendron (Fig. 513), Languria (Fig. 522), Megalodacne (Fig. 523), Derobrachus (Fig. 558), and others. The supratentorium is a surprisingly persistent structure considering the large number of genera that possess it in a more or less rudimentary state. The broken ends of the tentoria of Eupsalis (Fig. 573), Lixus (Fig. 580), and Sphenophorus (Fig. 582), are expanded, which expansion may include a part of the supratentoria. This seems reasonable to believe when a rudimentary one is evidently present in Rhynchites (Fig. 577) and Attelabus (Fig. 578). Sphenophorus is peculiar in having the lateral margins of the tentoria fused to the oculata. The head-capsule of this genus is suddenly constricted at this point, which probably placed the tentorium and head-wall in contact, a fusion finally resulting. The supratentoria of Cucujus (Fig. 520) and Passalus (Fig. 556) are stout structures, but extremely short. In the former, this condition is due to the flatness of the head, in the latter, to the unusually close proximity of a part of the pretentoria to the dorsal surface.

SOME PHYLOGENETIC CONSIDERATIONS

With the hypothetical type of coleopterous head in mind, it is possible to note the lines of development that have taken place within the various groups. Structures have developed away from the primitive condition with varying degrees of rapidity, and sometimes in different directions. It is difficult from this study to decide on the amount of importance to attach to the change that may take place in a particular structure, and to average the degree of primitiveness as a whole of the development of the structures characteristic of a group, and to indicate with precision the place in the primitive scale of each group. As previously mentioned, owing to the wide field covered in this investigation it was impossible to find time to study a large representation of genera within each family. Such a study should help one considerably in reaching clearer conclusions as to the arrangement of the genera in the primitive scale. Using this study as a basis, it is quite possible, however, to discuss the relative importance of the structural changes exhibited by the different groups, and to suggest possible inconsistencies in the present arrangement of certain genera. Statements made in the following discussion are based only on this study.

The characteristic possession by the Adephaga (Figs. 2–10, 23–24, 150–158, 297–305, 444–452) of the occipital suture, of complete epicranial arms, of a generalized position of the antennariae and of the pretentorinae, of a generalized form of labrum, and of tentorium, would force such families as the Cicindelidae, Carabidae, Amphizoidae and Omophronidae into a primitive place in the phylogenetic scale, in spite of their specialized ventral surface. No other large group shows as many primitive characters. The genera of the above mentioned families show a great similarity in all their structures and must be closely related. Of these families Omophronidae possibly possesses the most generalized dorsal surface, though the occipital suture in Omophron is not nearly complete, and does not show on this surface. Omophron can hardly hold an intermediate position between the Carabidae and the Haliplidae, for the latter family, as represented by Peltodytes, shows little similarity with any other family of the Adephaga. The form of the head is distinctly specialized, being globular, with enormous eyes, and the mouth-parts and the very small labrum are directed distinctly ventrad. The occipital suture is probably lacking, the epicranial suture is shorter than in any other genus of the Adephaga. On the ventral surface, the metatentorinae extend only half-way between the oc-

cipital foramen and the submentum, and the gular sutures extend no farther cephalad, whereas in all the other genera of the Adephaga the metatentorinae are close to the submentum and complete gular sutures are present. Finally, the tentorium of Peltodytes is not so well developed, and the supratentoria are small and do not reach the ental surface of the head-wall. In all other genera of the Adephaga the tentorium is large and strongly chitinized in all its parts. The Dytiscidae and Gyrinidae are very similar fundamentally, and differ from other adephagous families in the position on the ventral aspect of such structures as the antennariae and the pretentorinae, and by a rudimentary or absent occipital suture. The instability of the epicranial suture is well illustrated by the case of the two closely related genera, Dytiscus and Cybister, the former possessing complete, distinct arms, and a considerable part of the caudal end of the stem, the latter incomplete and rather indistinct arms and no part of the stem. The Dytiscidae and the Gyrinidae are undoubtedly more specialized than the first four families of the Adephaga.

The Hydrophiloidea (Figs. 11–14, 159–166, 306–309, 453–456) show by the form and texture of the heads of Hydrous and Hydrophielus that they are quite similar to those of the Dytiscidae and Gyrinidae, being broad and short, and strongly chitinized. The antennariae and pretentorinae of these two species have migrated ventrad, as in the other two families. The metatentorinae, the gula, and the tentorium are also almost identical in form and condition. These species are evidently very closely related to the Dytiscidae and Gyrinidae. Hydraena is not so similar, the dorsal surface of its head being more like that of the typical Carabidae in shape and position of the parts. The gular sutures are short, as in Peltodytes. The head of Hydroscapha, its shape, the course of the epicranial arms, position of pretentorinae and antennariae, is distinctly like that of Omophron.

The genera of the Silphoidea (Figs. 15–21, 163–169, 310–316, 457–462) show many inconsistencies. The dorsal and ventral surfaces and the endoskeleton of no two genera are nearly alike. Necrophorus possesses the most generalized dorsal surface, which is very like that of the first four families of the Adephaga; Clambus, perhaps the most specialized, being distinctly consolidated. On the other hand, Necrophorus possesses the most specialized ventral surface present in this superfamily. The gular sutures are complete, and for more than half their extent meet on the meson. In contrast, there are practically no gular sutures in Connophron, a scydmaenid, and Molamba, a corylophid. No greater extremes of this surface can be found within the limits of any other superfamily. The tentorium exhibits just as great extremes in development. That of Leptinus is quite generalized; that of Necrophorus well developed but specialized, owing to the invagination of the gula; that of Connophron with no corpotentorium

nor laminatentorium and rudimentary supratentorinae; that of Molamba the most rudimentary tentorium of any genus included within this study. No clearer illustration of the difficulties of indicating relationship can be shown than that exhibited by the families of the Silphoidea.

A study of the Staphylinoidea (Figs. 22, 25-35, 170-181, 317-328, 463-473) shows that the various genera of the Staphylinidae have considerable homogeneity. Tachinus departs the most from the characteristic condition, in possessing a much more generalized dorsal surface than the other members of this family. The Staphylinidae possess a tentorium and a ventral surface similar on the whole to that of the Adephaga and the Hydrophiloidea. Tachinus, through the added similarity of its dorsal surface, would seem to bear a particularly close relationship to these groups. The Sphaeriidae, as represented by Sphaerius, and the Ptilidae, as represented by Limulodes, possess a primitive condition of the metatentorinae, while Scaphidium and Hister possess confluent gular sutures. The Pselaphidae, as represented by Pilopius, and the Clavigeridae, as represented by Fustiger, in form of head and character of the ventral surface and tentorium show a close relationship to Connophron. The irregularities of structure displayed by the families of this group are nearly as great as those displayed by the families of the Silphoidea. Both of these superfamilies probably need considerable revising.

All of the genera of the Cantharoidea (Figs. 36-42, 182-190, 329-335, 474-480) possess complete epicranial arms and dorsal portion of the antennariae, and lack of corpotentorium, except the Cleridae and the Corynetidae, represented by Trichodes and Necrobia respectively. All possess a complete gula except the latter genera and Collops, the representative of the Melyridae. This superfamily can be divided into three subgroups. One group will include the Lycidae and Lampyridae, characterized by a globular head, short broad gula, and absence of the pretentorinae. A second group will include the Phengodidae and the Cantharidae, characterized by a longer and flatter head and longer gula. The third group will include the Cleridae and the Corynetidae, possessing short incomplete arms, incomplete gular sutures, and a well developed corpotentorium. Collops does not seem to fit in very well anywhere, though this genus, through the form of its dorsal surface and tentorium may possibly lean towards the second group. Cantharis, of the second group, is peculiar in possessing a normal gula, whereas in the other forms the gula is rudimentary, though in all other respects this genus is like the other members of this group. The first and second groups are no doubt closely related. The latter is probably the more generalized, possessing a dorsal surface resembling to a marked extent the dorsal surface of the Carabidae. The gula, in so far as it is complete, also resembles the condition of this structure in the families of the Adephaga, and particularly in Necrophorus, of the

Silphoidea. It has, however, developed much farther, even, than in Necrophorus, being not only invaginated, but reduced to a more or less rudimentary state. The first group probably evolved from the second by the change in the shape of the head, due to the enormous development of the compound eyes and the loss of much of the gular region, which has probably fused with the cervix. Parallel with these changes, the pretentoria shifted their position so that they could better support the globular head, and came to assume the direction ordinarily assumed by the supratentoria of other genera. The third group would appear to be more closely related to the Mordelloidea than to this superfamily. The condition of the epicranial suture, the position of the antennariae, pretentorinae, and metatentorinae, the degree of development of the gula and tentorium, would all favor this assumption.

The representatives of the Lymexyloidea (Figs. 43–44, 191–192, 336–337, 481), two families of this group, are not very similar. Hylecoetus has a head that is fairly compact, directed a little ventrad, the cervix possessing a cervepisternum, and a well developed tentorium. The head of Micromalthus is more compact than that of Hylecoetus, directed cephalad, there is no sclerite in the cervix, and the tentorium is rudimentary. As the superfamily stands, both could be placed in the Cucujoidea.

The representative of the Cupesoidea (Figs. 45, 193, 338, 482) studied does not show any particular peculiarities of structure of the head that would entitle it to be placed in a separate superfamily. It can be very readily included with the Mordelloidea, for approximately the same reasons as the Cleridae and Corynetidae.

The genera of the Mordelloidea (Figs. 46–57, 194–205, 339–350, 483–494) show considerable homogeneity. Most of them possess heads that are elongate, with a generalized dorsal surface and a large postclypeus and labrum, both on the same general level with the rest of the dorsal surface. The epicranial suture, however, shows considerable instability, sometimes showing complete arms and stem, as in Epicauta, while in others the epicranial suture may be extremely reduced, as in Macrosiagon. If these two genera are at all related, the condition of the epicranial suture can hardly throw any light on the degree of relationship. On the other hand, the metatentorinae are stable in position, and are located almost uniformly about half-way between the occipital foramen and the submentum. Another characteristic feature is the fact that most of the genera possess heads that are distinctly constricted at their caudal ends to form a neck. The Oedemeridae, the Cephaloidae, the Pyrochroidae, the Pedilidae, the Anthicidae, and possibly the Cupesidae and Meloidae, seem particularly closely related, through the possession of similarly shaped heads, whose caudal ends are distinctly constricted, of a generalized dorsal

surface, of compound eyes that are usually more or less emarginated, of a ventral surface whose structures are practically in a similar condition, and of a tentorium that is alike throughout, with the exception of the Meloidae, in which the corpotentorium is absent. Though the dorsal surface of the Mordelloidea resembles to a considerable extent that of such families as the Carabidae and Cantharidae, yet this surface differs so widely in closely related groups that we can hardly place too much importance on the resemblance here. What seems to be far more important is the totally different condition of the ventral surfaces in the Mordelloidea and the Carabidae, for instance. In the former the gular sutures and the metatentorinae extend uniformly half way between the occipital foramen and the submentum; in the Carabidae the gular sutures extend the whole distance between these parts and the metatentorinae, nearly to the submentum. The Mordelloidea and such groups as the Adephaga and Hydrophiloidea do not appear to be nearly related.

The members of the Elateroidea are on the whole (Figs. 58–64, 206–212, 351–357, 495–501) homogeneous with the exception of the Buprestidae. The pretentorinae and the antennariae are located on the dorsal surface, and the epicranial arms extend no farther caudad than the pretentorinae. On the ventral aspect, the metatentorinae extend but little cephalad of the occipital foramen, and the gular sutures no farther. The corpotentorium is lacking in all except Cebrio and Euthysanius. In the Buprestidae, on the other hand, the pretentorinae and antennariae have migrated distinctly ventrad, and are not visible at all from the dorsal surface. The gular sutures extend the whole distance between the occipital foramen and the submentum, and there is a distinct corpotentorium. Considering these points, the Buprestidae are hardly closely related to the rest of the Elateroidea.

With the exception of the Georyssidae, the members of the Dryopoidea (Figs. 65–69, 213–217, 358–362, 502–506) appear to be fairly homogeneous. The chief characteristics are very prominent widely separated metatentorinae, located very near the occipital foramen, and a very broad submentum. The ventral surface of the Georyssidae, as represented by Georyssus, is totally different. In this family the gular sutures extend nearly to the submentum, and are confluent through practically their entire extent. The metatentorinae cannot be definitely located. Georyssus would appear to be related to Hister, both through the condition of the gula, of the tentorium, and of the dorsal surface. The general appearance of the ventral surface in the Dryopoidea is much like that of the Elateroidea, and in other characteristics they are not unlike. These two superfamilies are probably related.

The representatives of the four families of the Dascilloidea (Figs. 70–73, 218–221, 363–366, 507–510) studied are similar in structure. There

are no outstanding features that would warrant placing them in a separate superfamily. They are negative enough in their characteristics to fit in, perhaps, in a number of other superfamilies, such as the Mordelloidea, Cucujoidea, and Tenebrionoidea.

The representatives of the three families of the Byrrhoidea (Figs. 74–76, 222–224, 367–369, 511–513), the Dermestidae and the Byrrhidae studied, Dermestes and Byrrhus, do not seem to differ decidedly from one another, but the Nosodendronidae, represented by Nosodendron, may fit in better in some other group, such as the Dryopoidea. They resemble the members of this latter group in the position of the metatentorinae and in the form of the submentum. In Nosodendron, the metatentorinae are almost adjacent to the occipital foramen, with a membranous area included between them. That part of the metatentorium surrounding the periphery of the occipital foramen projects deep into the head. The supratentoria are well developed. None of these characteristics are possessed by the other two genera studied.

The representative of the single family of this superfamily (Figs. 77, 225, 370, 514) studied, Rhysodes, shows distinct peculiarities in the structure of its head, such as an extremely thick chitinous head-wall, a fibrous condition of the cervix, an arrow-shaped head, enormously developed submentum, and very small mouth-parts. Its relationships are not at all clear.

The members of the Cucujoidea (Figs. 78–98, 226–246, 371–391, 515–535) show on the whole a short broad head-capsule, a distinct ventral migration of the antennariae and pretentorinae, the degeneration of the epicranial arms, and a slight migration of the metatentorinae from the occipital foramen. There is some variation in the dorsal aspect. The genera belonging to the Mycetophagidae, the Mycetaeidae, the Melanophthalmidae, the Endomychidae, and perhaps those of a few other families, possess dorsal surfaces that strongly resemble the dorsal surface of the Mordelloidea. In Derodontus and Philothermus, a colydiid, the antennariae and the pretentorinae are both on the dorsal aspect, located considerably caudad. The ventral aspect of all the members of the group, however, is strikingly similar. The tentorium is fairly uniform throughout the group except in Tenebroides and Phalacrus, in which the pretentorium has distinctly degenerated, due probably to the heavy chitinization of the head-wall. In the shape of the head and the condition of the metatentorinae and the gular sutures, the Cucujoidea show a similarity to the Mordelloidea, and to the superfamily Tenebrionoidea.

There are no particular characteristics of the head-capsule that would separate the Tenebroidea (Figs. 99–111, 247–259, 392–404, 536–548) from the typical Mordelloidea. For instance, the dorsal and ventral surfaces and the endoskeleton of Arthromacra, Pseudocistela, and Penthe,

are almost exactly like these parts of such genera of the Mordelloidea as Epicauta, Cephaloon, and Macratria. The corpotentorium of Arthromacra and Epicauta is, however, lacking. The structure of the various parts of the head-capsule of the representatives of the Bostrichidae varies considerably. The epicranial arms are complete in Bostrichus, Lyctus, Plesiocis, and Sphindus. With the exception of Sphindus these families show a distinct ventral migration of the antennariae and pretentorinae. In contrast, Ptinus and Sitodrepa do not possess complete arms, and the antennariae and pretentorinae are located more dorsad, markedly so in the former. On the ventral surface, there is considerable variation in the position of the metatentorinae. The tentorium also varies a great deal. This is probably not a very homogeneous group. Sphindus seems to be structurally more similar to Sphaerius than any other genus studied.

The Scarabaeoidea (Figs. 112–119, 260–267, 405–413, 549–556) is a very homogeneous group, characterized by a heavy chitinization of the head-wall, degeneration of the epicranial suture, ventral migration of the antennariae and the pretentorinae, and a complete gula, except in Pseudolucanus, in which the gular sutures extend no more than half the distance between the occipital foramen and the submentum. In the development of the ventral surface and perhaps the tentorium, the Scarabaeoidea should be classed with the Adephaga and related groups.

The Cerambycoidea (Figs. 120–135, 268–283, 414–429, 562–572) is also a very homogeneous group, characterized by a weak chitinization of the head-wall, a distinct dorsal position of the antennariae and the pretentorinae, and a more or less well developed epicranial suture. The gular sutures are generally short. The tentorium is delicate and membranous throughout.

The members of the Rhynchophora (Figs. 136–148, 284–296, 430–442, 573–585) may or may not possess a snout. They may or may not possess confluent gular sutures. When they do, the condition is the same as in other Coleoptera, except that the invaginations are apt to be more extensive. They may or may not possess a labrum. There is no definite character of the head-capsule by which the Rhynchophora as a group can be separated from other Coleoptera. The affinities of this group are not at all clear.

The condition of the dorsal surface throughout the groups is most variable, and can be relied upon but little to furnish evidence of the degree of relationship. On the ventral surface the condition is much more stable, and probably much more reliable in indicating affinities. The tentorium is less variable than the dorsal surface, and less stable than the ventral surface. Weighing the evidence presented in this study, two large groups of most of the families can be made. The Lymexyloidea, the Cupesoidea, the Mordelloidea, the Elateroidea, the Dryopoidea, the Dascilloidea, the Byrrhoidea, the Cucujoidea, the Tenebrionoidea,

and the Bostrichoidea should probably be grouped together, while the characteristic families of the Cantharoidea, the Staphylinoidea, and the Silphoidea should perhaps be grouped with the Adephaga and Hydrophiloidea. The Scarabaeoidea may also be included in this latter group. The affinities of the Cerambycoidea and the Rhynchophora are too vague to include either in the two larger groups.

SUMMARY

1. This investigation deals with the homology of all the structures of the head-capsule of one or more representatives of one hundred and five of the one hundred and nine families of Coleoptera listed by Leng in his recent catalogue. One hundred and forty-six genera have been studied and figured, nearly all representing different important subgroups.

2. This serial study has made it possible to identify the same structures in a wide series of forms, and to definitely fix the homology of all the parts of the head-capsule.

3. Hypothetical types have been constructed, based on the structure of the head-capsule of generalized insects and Coleoptera. These show the Coleoptera to have developed in general a consolidation of sclerites and a heavier chitinization of the head wall, a compacting of the head as a whole, and an approximation of the dorsal and ventral movable parts at the cephalic end.

4. The epicranial suture has been identified in all but two of the genera studied. It has proved a great aid in determining the limits of neighboring parts. What may appear to be a distinct epicranial suture may not even be a suture. It is sometimes distinctly invaginated. Its identity can only be definitely fixed by determining the location of the pretentorinae, which are always associated with it.

5. The limits of the vertex are dependent upon the position of the epicranial suture. In the Rhynchophora nearly all of the snout belongs to the vertex.

6. The unmodified occipital suture has been identified only in the Adephaga. The cephalic end on the ventral surface is always represented by part of a curving ridge, which is present in all but a few genera.

7. The supratentorinae have been identified in a few genera, nearly all of which belong to the Staphylinoidea.

8. The pretentorinae are the great landmarks of the head-capsule and have been identified in all but two genera. They are, in the vast majority of genera, located near the cephalic end of the epicranial arms. A definite determination of the pretentorinae cannot always be made without an ental examination of the head.

9. The size and form of the front is dependent upon the position of the epicranial arms. In the Cerambycoidea it is large. In many genera, as illustrated by Omophron, Harpalus, and Tachinus, it is partly or wholly invaginated. It may probably be rudimentary or wholly lost in many genera in which the mesal parts of the epicranial arms have disappeared.

10. What has been called the clypeal suture in such genera as Cicindela and Harpalus is not even a suture, but the line of invagination of the front.

11. The clypeus is always divided into the postclypeus and the preclypeus. The preclypeus is with one exception always distinctly membranous. It may be as large or larger than the labrum.

12. There is a distinct clypealia present in the Coleoptera and in widely separated groups, such as the Adephaga and the Cerambycoidea.

13. The labrum may be indistinctly determined in both Rhynchophora and other Coleoptera. It may also be quite distinct in some Rhynchophora where it is considered to be absent.

14. The submentum is always located distinctly cephalad of the occipital foramen, with a chitinized area between it and the foramen.

15. The metatentorinae may be located on the cephalo-lateral border of the occipital foramen, as in generalized insects, or they may be far cephalad of this location.

16. All that region between the occipital foramen and the submentum is a part of the postgenae, produced by the fusion on the meson of the mesal margins of the postgenae.

17. The gular sutures result from the cephalic migration of the metatentorinae.

18. The gula is that area included between the gular sutures, and is, therefore, derived from the postgenae. The majority of the Coleoptera possess a gula that extends no more than half the distance between the occipital foramen and the submentum.

19. The tentorium of the Coleoptera is typically quite similar in form and development to that of generalized insects. Frequent modifications are loss of chitinization, loss of corpotentorium and laminatentorium. Occasionally the pretentorium may be rudimentary. The functions of the absent parts are assumed by other parts of the tentorium, or by the pharynx, or the head may be so compact and chitinized that a tentorium is no longer needed.

20. The cephalic migration of the submentum, and the subsequent formation of an indistinguishable area between it and the occipital foramen is due either to the migration caudad of the occipital foramen or to the cephalic pull on the mouth-parts or to both. The cephalic migration of the metatentoria and, therefore, the metatentorinae, with consequent production of the gula, is probably due to the cephalic pull on the tentorium to furnish a firmer support for the muscles and tendons of the mouth-parts.

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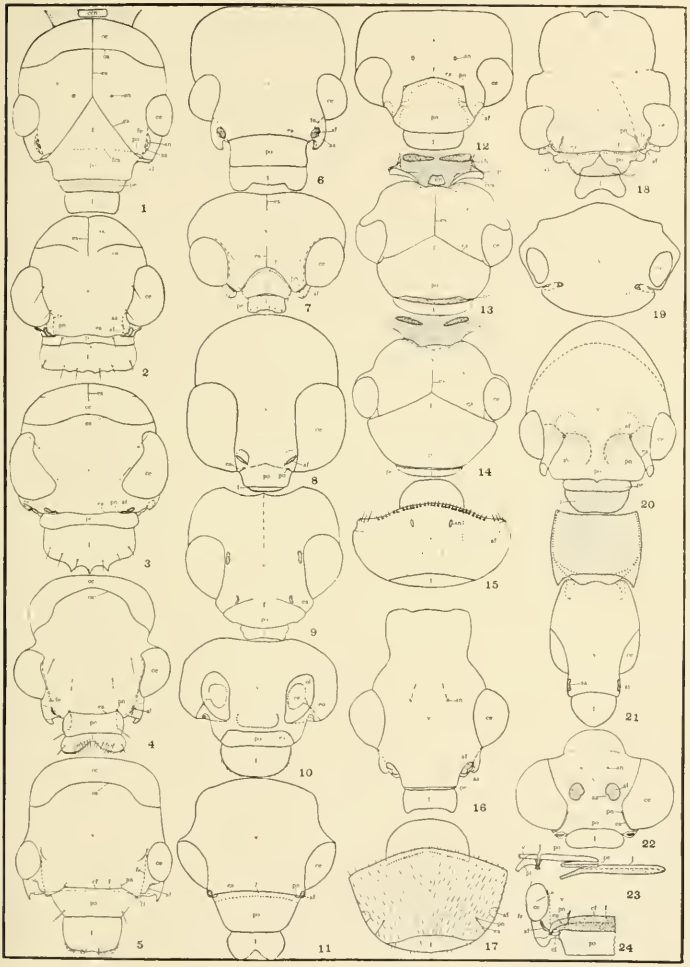
PLATE I

EXPLANATION OF PLATE I

DORSAL ASPECT OF THE HEAD

Fig. 1. Hypothetical type.
Fig. 2. *Tetracha carolina.*
Fig. 3. *Cicindela formosa.*
Fig. 4. *Calosoma calidum.*
Fig. 5. *Harpalus erraticus.*
Fig. 6. *Amphizoa lecontei.*
Fig. 7. *Omophron americanum.*
Fig. 8. *Peltodytes 12-punctatus.*
Fig. 9. *Cybister fimbriolatus.*
Fig. 10. *Dineutes americanus.*
Fig. 11. *Hydraena marginicollis.*
Fig. 12. *Hydroscapha natans.*
Fig. 13. *Hydrous triangularis.*
Fig. 14. *Hydrophilus obtusatus.*
Fig. 15. *Platypsyllus castoris.*
Fig. 16. *Brathinus nitidus.*
Fig. 17. *Leptinus testaceus.*
Fig. 18. *Necrophorus carolinus.*
Fig. 19. *Clambus puberulus.*
Fig. 20. *Connophron fossiger.*
Fig. 21. *Molamba lunata.*
Fig. 22. *Stenus flavicornis.*
Fig. 23. *Harpalus erraticus*, cross-section of cephalic end of the dorsal aspect of the head.
Fig. 24. *Harpalus erraticus*, showing invagination of the front.

aa antacoila
af antafossa
an antacoria
ccn cervinotum
ce compound eye
cf clypofrons
cl clypealia
ea epicranial arm
eo exoculata
es epicranial stem
f front
fcs fronto-clypeal suture
fe frontal ridge
l labrum
oc occiput
ol oculata
os occipital suture
pe preclypeus
pn pretentorina
po postclypeus
sn supratentorina
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE I

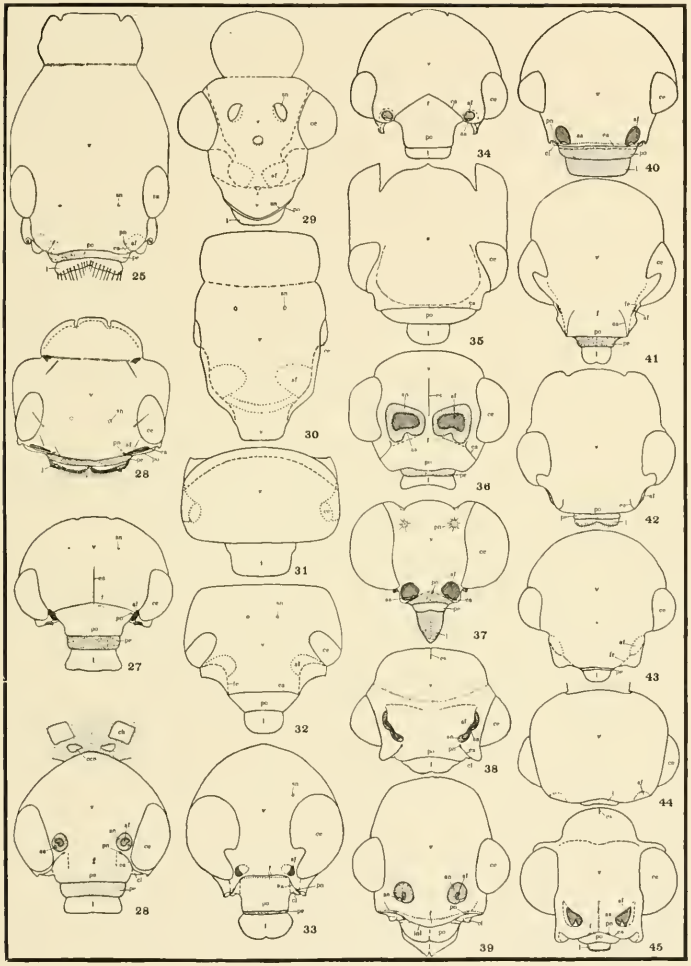
PLATE II

EXPLANATION OF PLATE II

DORSAL ASPECT OF THE HEAD

Fig. 25. *Gastrolobium bicolor.*
Fig. 26. *Creophilus villosus.*
Fig. 27. *Tachinus fimbriatus.*
Fig. 28. *Aleochara lata.*
Fig. 29. *Pilopius lacustris.*
Fig. 30. *Fustiger fuchsi.*
Fig. 31. *Limulodes paradoxus.*
Fig. 32. *Sphaerius politus.*
Fig. 33. *Scaphidium quadriguttatum.*
Fig. 34. *Sphaerites glabratus.*
Fig. 35. *Hister memnonius.*
Fig. 36. *Calopteron terminale.*
Fig. 37. *Photinus pyralis.*
Fig. 38. *Phengodes plumosa.*
Fig. 39. *Chauliognathus pennsylvanicus.*
Fig. 40. *Collops nigriceps.*
Fig. 41. *Trichodes nuttalli.*
Fig. 42. *Necrobia rufipes.*
Fig. 43. *Hylecoetus lugubris.*
Fig. 44. *Micromalthus debilis.*
Fig. 45. *Cupes concolor.*

aa antacoila
af antafossa
an antacoria
ccn cervinotum
ce compound eye
cl clypealia
ea epicranial arm
es epicranial stem
f front
fe frontal ridge
l labrum
pe preclypeus
pn pretentorina
po postclypeus
sn supratentorina
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE II

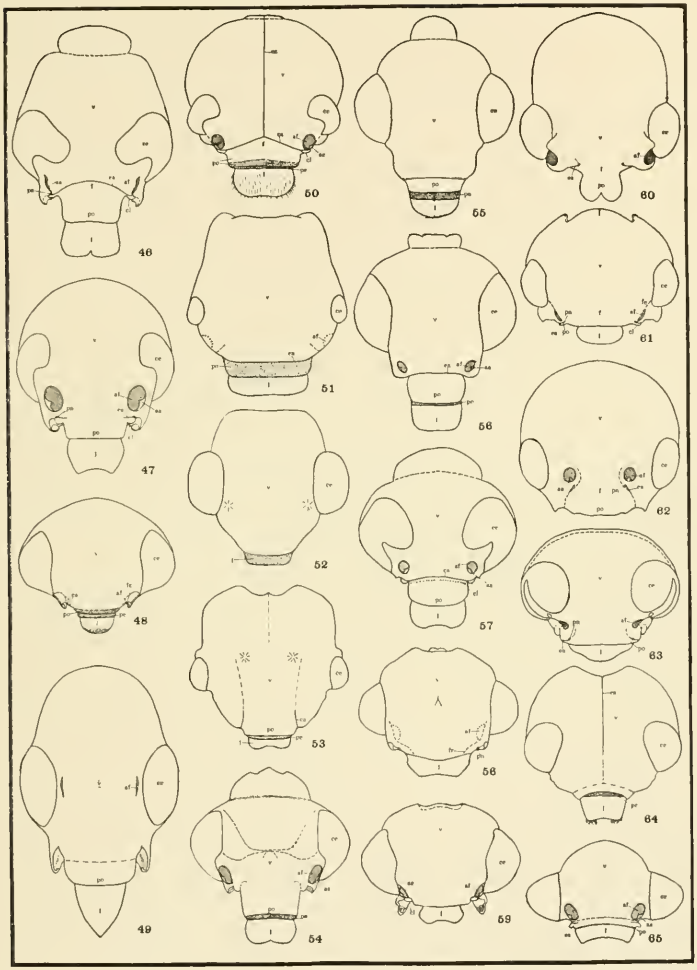
PLATE III

EXPLANATION OF PLATE III

DORSAL ASPECT OF THE HEAD

Fig. 46. *Cephaloon lepturides.*
Fig. 47. *Nacerda melanura.*
Fig. 48. *Tomoxia bidentata.*
Fig. 49. *Macrosiagon dimidiatum.*
Fig. 50. *Epicauta marginata.*
Fig. 51. *Eurystethus debilis.*
Fig. 52. *Othnius* sp.
Fig. 53. *Pytho planus.*
Fig. 54. *Neopyrochroa flabellata.*
Fig. 55. *Macratria murina.*
Fig. 56. *Notoxus anchora.*
Fig. 57. *Zonantes fasciatus.*
Fig. 58. *Cebrio bicolor.*
Fig. 59. *Euthysanius lautus.*
Fig. 60. *Sandalus niger.*
Fig. 61. *Alaus oculatus.*
Fig. 62. *Isorhipis ruficornis.*
Fig. 63. *Throscus chevrolati.*
Fig. 64. *Chalcophora virginiensis.*
Fig. 65. *Psephenus lecontei.*

aa antacoila
af antafossa
ce compound eye
cl clypealia
ea epicranial arm
es epicranial stem
f front
fr frontal ridge
l labrum
pe preclypeus
pn pretentorina
po postclypeus
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE III

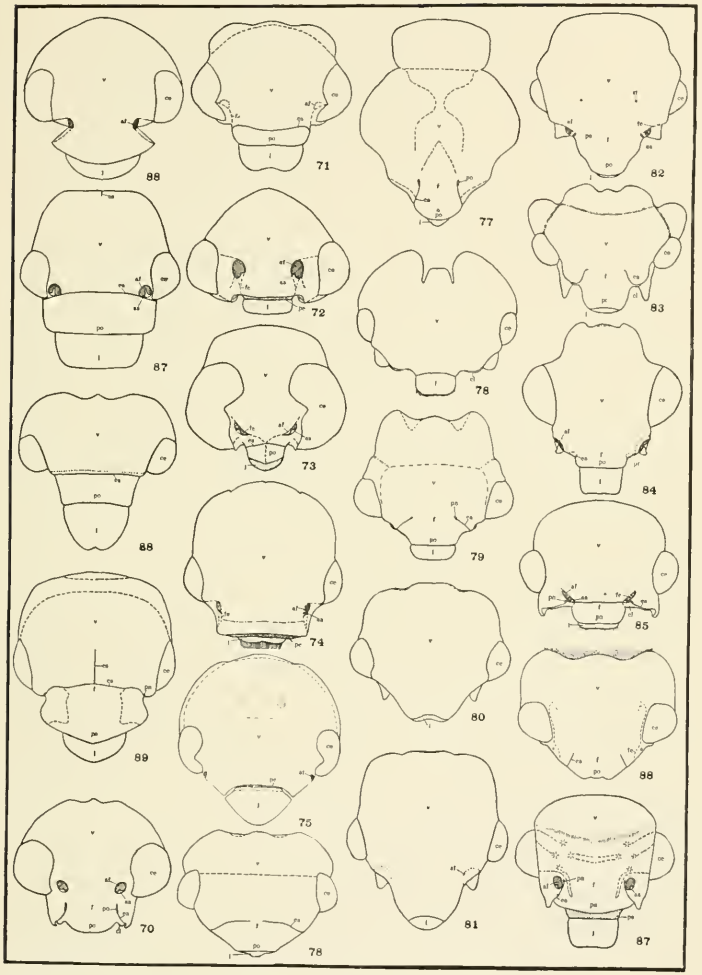
PLATE IV

EXPLANATION OF PLATE IV

DORSAL ASPECT OF THE HEAD

Fig. 66. *Helichus striatus.*
Fig. 67. *Stenelmis sinuata.*
Fig. 68. *Hetcroeerus undatus.*
Fig. 69. *Georyssus californicus.*
Fig. 70. *Eurypogon niger.*
Fig. 71. *Eucinetus morio.*
Fig. 72. *Cyphon ruficollis.*
Fig. 73. *Chelonarium errans.*
Fig. 74. *Dermestes lardarius.*
Fig. 75. *Byrrhus americanus.*
Fig. 76. *Nosodendron unicolor.*
Fig. 77. *Rhysodes americanus.*
Fig. 78. *Tenebroides sinuatus.*
Fig. 79. *Phenolia grossa.*
Fig. 80. *Glischrochilus fasciatus.*
Fig. 81. *Rhizophagus bipunctatus.*
Fig. 82. *Phyconomus marinus.*
Fig. 83. *Cucujus clavipes.*
Fig. 84. *Hemipeplus marginipennis.*
Fig. 85. *Languria mozardi.*
Fig. 86. *Megalodacne fasciata.*
Fig. 87. *Derodontus asculatus.*

aa antacoila
af antafossa
ce compound eye
el clypealia
ea epicranial arm
es epicranial stem
f front
fe frontal ridge
l labrum
p preclypeus
pn pretentorina
po postclypeus
pr precoila
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE IV

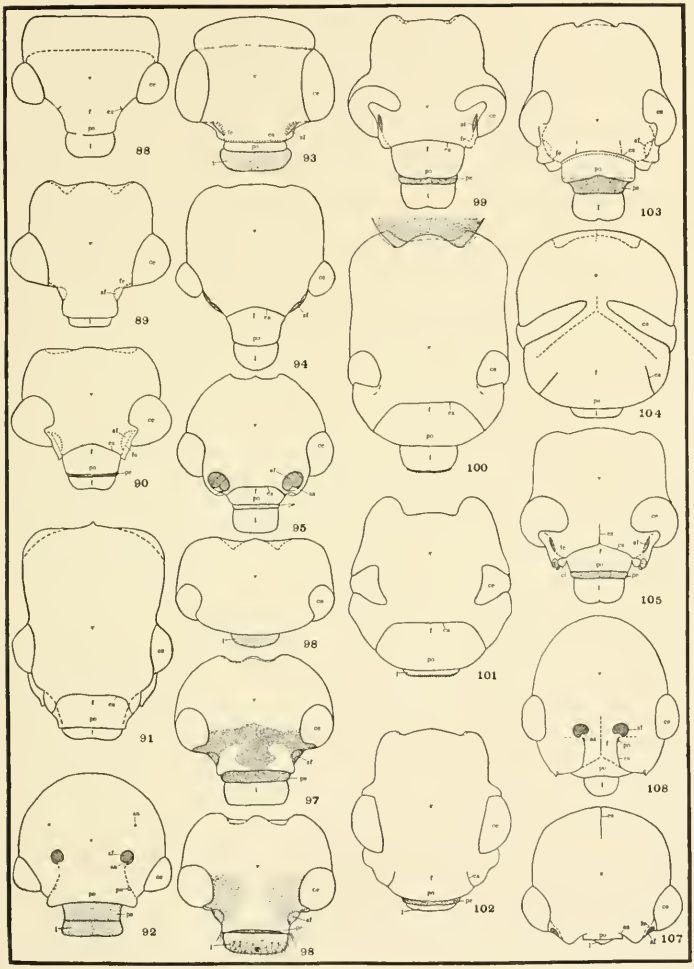
PLATE V

EXPLANATION OF PLATE V

DORSAL ASPECT OF THE HEAD

Fig. 88. *Anchicera ephippiata.*
Fig. 89. *Byturus unicolor.*
Fig. 90. *Mycetophagus punctatus.*
Fig. 91. *Bothrideres geminatus.*
Fig. 92. *Philothermus glabriculus.*
Fig. 93. *Melanophthalma cavicollis.*
Fig. 94. *Phymaphora pulchella.*
Fig. 95. *Endomychus biguttatus.*
Fig. 96. *Phalacrus politus.*
Fig. 97. *Hippodamia convergens.*
Fig. 98. *Adalia bipunctata.*
Fig. 99. *Pseudocistela brevis.*
Fig. 100. *Alobates pennsylvanica.*
Fig. 101. *Tenebrio molitor.*
Fig. 102. *Boros unicolor.*
Fig. 103. *Arthromacra aenea.*
Fig. 104. *Hyporphagus* sp.
Fig. 105. *Penthe obliquata.*
Fig. 106. *Ptinus brunneus.*
Fig. 107. *Sitodrepa panicea.*

aa antacoila
a antafossa
e compound eye
l clypealia
a epicranial arm
s epicranial stem
f front
fe frontal ridge
l labrum
pe preclypeus
pn pretentorina
po postclypeus
sn supratentorina
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE V

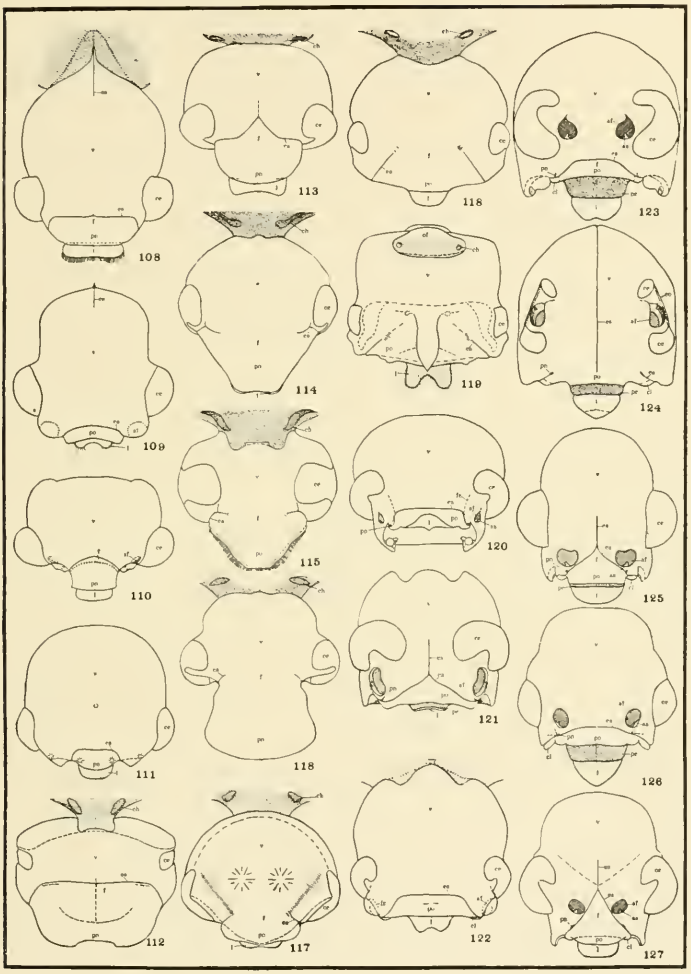
PLATE VI

EXPLANATION OF PLATE VI

DORSAL ASPECT OF THE HEAD

Fig. 108. *Bostrichus bicornis.*
Fig. 109. *Lyctus planicollis.*
Fig. 110. *Sphindus americanus.*
Fig. 111. *Plesiocis cribrum.*
Fig. 112. *Aphodius fimetarius.*
Fig. 113. *Dichelonyx elongata.*
Fig. 114. *Pelidnota punctata.*
Fig. 115. *Strategus julionus.*
Fig. 116. *Osmoderma eremicola.*
Fig. 117. *Trox suberosus.*
Fig. 118. *Pseudolucanus capreolus.*
Fig. 119. *Passalus cornutus.*
Fig. 120. *Parandra brunnea.*
Fig. 121. *Derobrachus brunneus.*
Fig. 122. *Spondylis buprestoides.*
Fig. 123. *Glycobius speciosus.*
Fig. 124. *Tetraopes tetraophthalmus.*
Fig. 125. *Donacia piscatrix.*
Fig. 126. *Syneta ferruginea.*
Fig. 127. *Criocerus asparagi.*

aa antacoila
af antafossa
ce compound eye
ch chitinized area
cl clypealia
ea epicranial arm
eo exoculata
es epicranial stem
f front
fe frontal ridge
l labrum
pe preclypeus
pn pretentorina
po postclypeus
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE VI

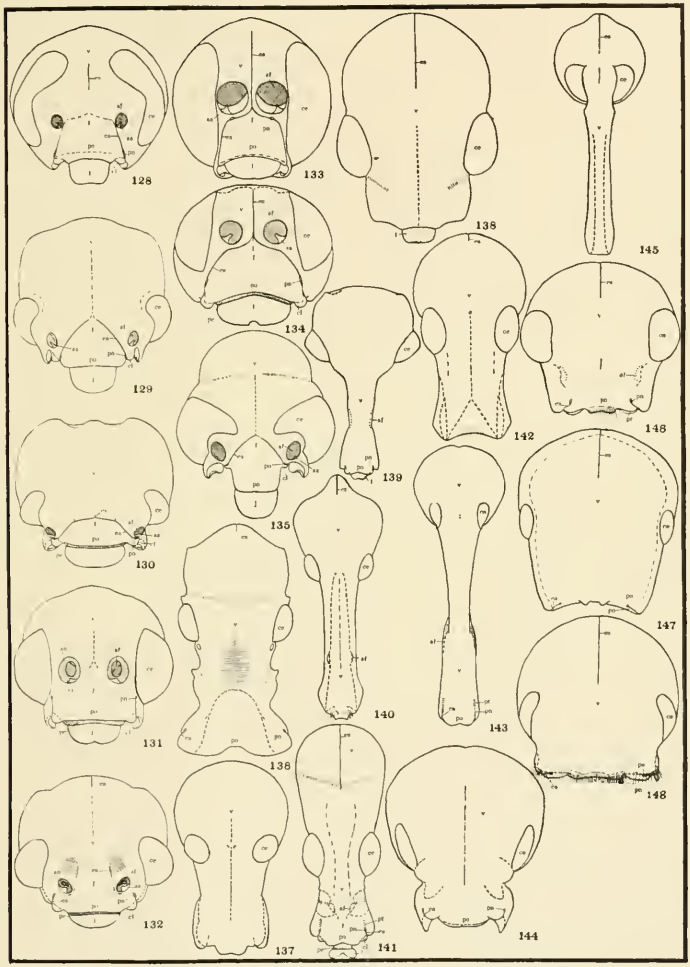
PLATE VII

EXPLANATION OF PLATE VII

DORSAL ASPECT OF THE HEAD

Fig. 128. *Cryptocephalus quadruplex.*
Fig. 129. *Chrysochus auratus.*
Fig. 130. *Leptinotarsa decemlineata.*
Fig. 131. *Diabrotica 12-punctata.*
Fig. 132. *Blepharida rhois.*
Fig. 133. *Anoplitis gracilis.*
Fig. 134. *Chelymorpha argus.*
Fig. 135. *Pachymerus gleditsiae.*
Fig. 136. *Eupsalis minuta.*
Fig. 137. *Ithycerus noveboracensis.*
Fig. 138. *Eurymycter fasciatus.*
Fig. 139. *Rhinomacer pilosus.*
Fig. 140. *Rhynchites bicolor.*
Fig. 141. *Attelabus analis.*
Fig. 142. *Epicaerus imbricatus.*
Fig. 143. *Lixus fimbriolatus.*
Fig. 144. *Thecesternus humeralis.*
Fig. 145. *Sphenophorus aequalis.*
Fig. 146. *Platypus flavicornis.*
Fig. 147. *Scolytus quadrispinosus.*
Fig. 148. *Dendroctonus valens.*

aa antacoila
af antafossa
an antacoria
ce compound eye
cl clypealia
ea epicranial arm
es epicranial stem
f front
l labrum
pe preclypeus
pn pretentorina
po postclypeus
pr precoila
pt pretentorium
v vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE VII

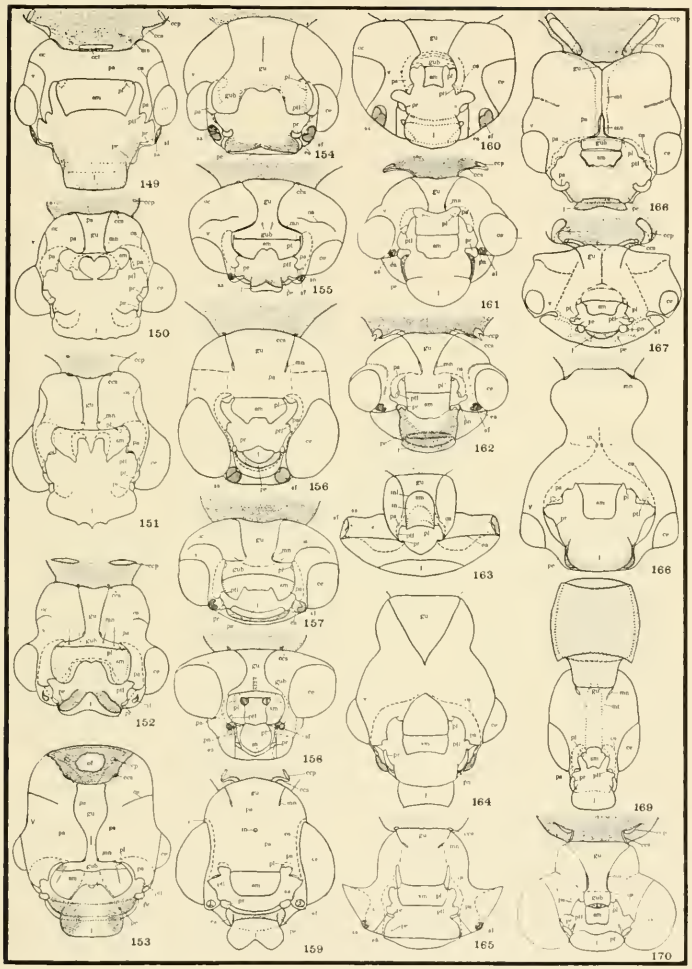
PLATE VIII

EXPLANATION OF PLATE VIII

VENTRAL ASPECT OF THE HEAD

Fig. 149. Hypothetical type.
Fig. 150. *Tetracha carolina.*
Fig. 151. *Cicindela formosa.*
Fig. 152. *Calosoma calidum.*
Fig. 153. *Harpalus erraticus.*
Fig. 154. *Amphizoa lecontei.*
Fig. 155. *Omophron americanum.*
Fig. 156. *Pelodytes 12-punctatus.*
Fig. 157. *Cybister fimbriolatus.*
Fig. 158. *Dineutes americanus.*
Fig. 159. *Hydraena marginicollis.*
Fig. 160. *Hydroscapha natans.*
Fig. 161. *Hydrous triangularis.*
Fig. 162. *Hydrophilus obtusatus.*
Fig. 163. *Platypsyllus castoris.*
Fig. 164. *Brathinus nitidis.*
Fig. 165. *Leptinus testaceus.*
Fig. 166. *Necrophorus carolinus.*
Fig. 167. *Clambus puberulus.*
Fig. 168. *Connophron fossiger.*
Fig. 169. *Molamba lunata.*
Fig. 170. *Stenus flavicornis.*

aa	antacoila	*mt*	metatentorium
af	antafossa	*oc*	occiput
an	antacoria	*os*	occipital suture
ccp	cervepimeron	*pa*	postgena
ccs	cervepisternum	*pe*	preclypeus
cct	cervisternum	*pl*	paracoila
ce	compound eye	*pn*	pretentorina
gu	gula	*pr*	precoila
gub	gula bar	*pt*	pretentorium
in	invagination	*ptl*	postcoila
inl	line of invagination	*sm*	submentum
l	labrum	*v*	vertex
mn	metatentorina		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE VIII

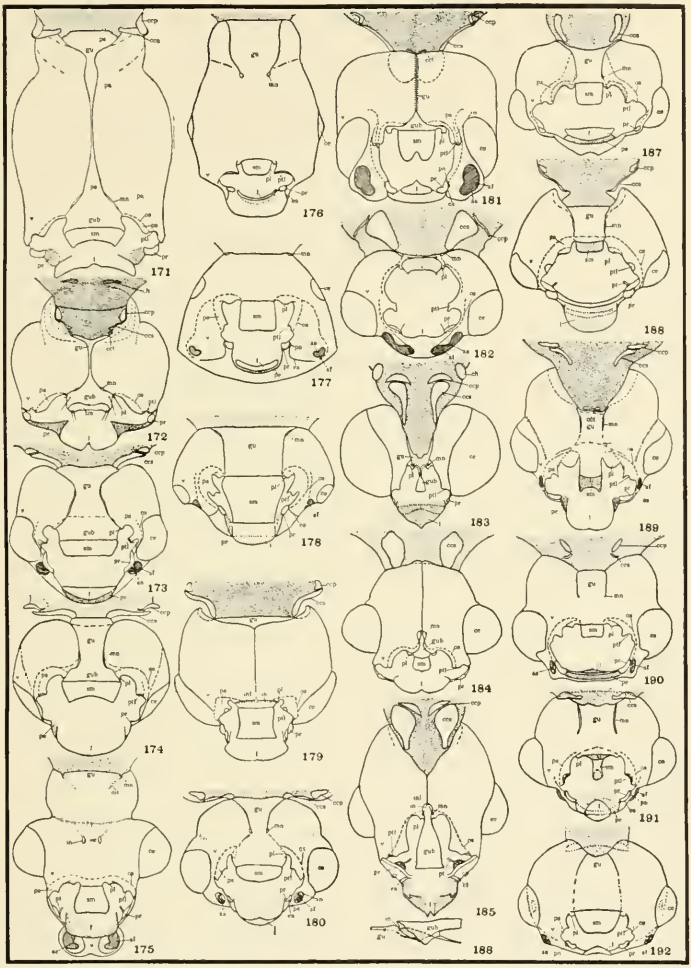
PLATE IX

EXPLANATION OF PLATE IX

VENTRAL ASPECT OF THE HEAD

Fig. 171. *Gastrolobium bicolor.*
Fig. 172. *Creophilus villosus.*
Fig. 173. *Tachinus fimbriatus.*
Fig. 174. *Aleochara lata.*
Fig. 175. *Pilopius lacustris.*
Fig. 176. *Fustiger fuchsi.*
Fig. 177. *Limulodes paradoxus.*
Fig. 178. *Sphaerius politus.*
Fig. 179. *Scaphidium quadriguttatum.*
Fig. 180. *Sphaerites glabratus.*
Fig. 181. *Hister memnonius.*
Fig. 182. *Calopteron terminale.*
Fig. 183. *Pholinus pyralis.*
Fig. 184. *Phengodes plumosa.*
Fig. 185. *Chauliognathus pennsylvanicus.*
Fig. 186. *Chauliognathus pennsylvanicus,* cross-section, showing invagination of gula.
Fig. 187. *Cantharis bilineatus.*
Fig. 188. *Collops nigriceps.*
Fig. 189. *Trichodes nutalli.*
Fig. 190. *Necrobia rufipes.*
Fig. 191. *Hylecoetus lugubris.*
Fig. 192. *Micromalthus debilis.*

aa	antacoila	*l*	labrum
af	antafossa	*mn*	metatentorina
an	antacoria	*mt*	metatentorium
ccp	cervepimeron	*os*	occipital suture
ccs	cervepisternum	*pa*	postgena
cct	cervisternum	*pe*	preclypeus
ce	compound eye	*pl*	paracoila
ch	chitinized area	*pn*	pretentorina
ea	epicranial arm	*pr*	precoila
gu	gula	*pt*	pretentorium
gub	gula bar	*ptl*	postcoila
in	invagination	*sm*	submentum
inl	line of invagination	*v*	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE IX

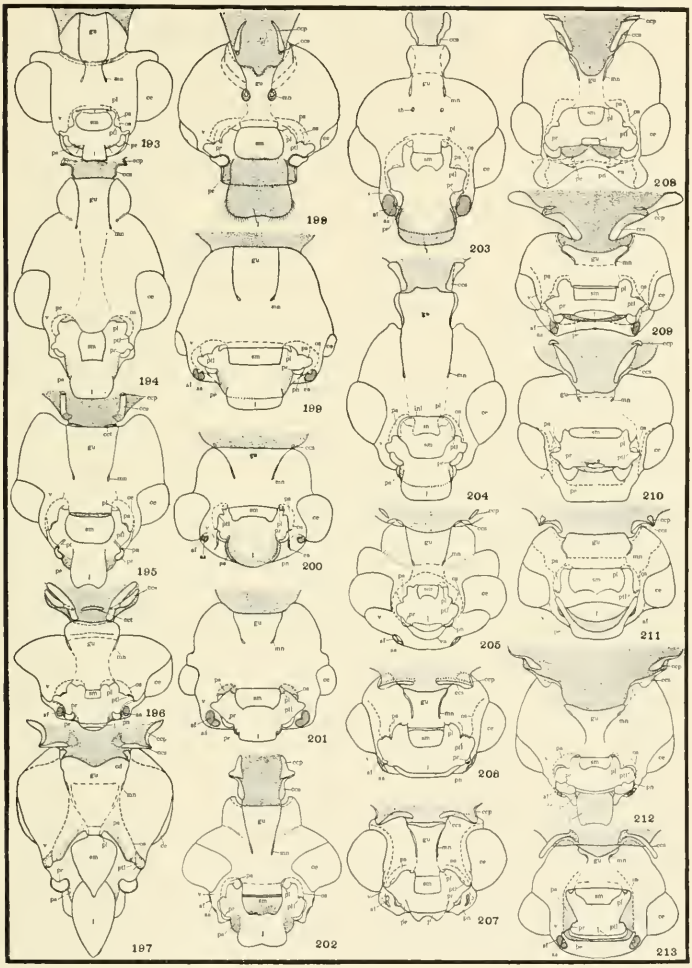
PLATE X

EXPLANATION OF PLATE X

VENTRAL ASPECT OF THE HEAD

Fig. 193. *Cupes concolor.*
Fig. 194. *Cephaloon lepturides.*
Fig. 195. *Nacerda melanura.*
Fig. 196. *Tomoxia bidentata.*
Fig. 197. *Macrosiagon dimidiatum.*
Fig. 198. *Epicauta marginata.*
Fig. 199. *Eurystethus debilis.*
Fig. 200. *Othnius* sp.
Fig. 201. *Pytho planus.*
Fig. 202. *Neopyrochroa flabellata.*
Fig. 203. *Macratria murina.*
Fig. 204. *Notoxus anchora.*
Fig. 205. *Zonantes fasciatus.*
Fig. 206. *Cebrio bicolor.*
Fig. 207. *Euthysanius lautus.*
Fig. 208. *Sandalus niger.*
Fig. 209. *Alaus oculatus.*
Fig. 210. *Isorhipis ruficornis.*
Fig. 211. *Throscus chevrolati.*
Fig. 212. *Chalcophora virginiensis.*
Fig. 213. *Pscphenus lecontei.*

aa	antacoila	*mn*	metatentorina
af	antafossa	*os*	occipital suture
ccp	cervepimeron	*pa*	postgena
ccs	cervepisternum	*pe*	preclypeus
cct	cervisternum	*pl*	paracoila
ce	compound eye	*pn*	pretentorina
ca	epicranial arm	*pr*	precoila
gu	gula	*ptl*	postcoila
in	invagination	*sm*	submentum
inl	line of invagination	*v*	vertex
l	labrum		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE X

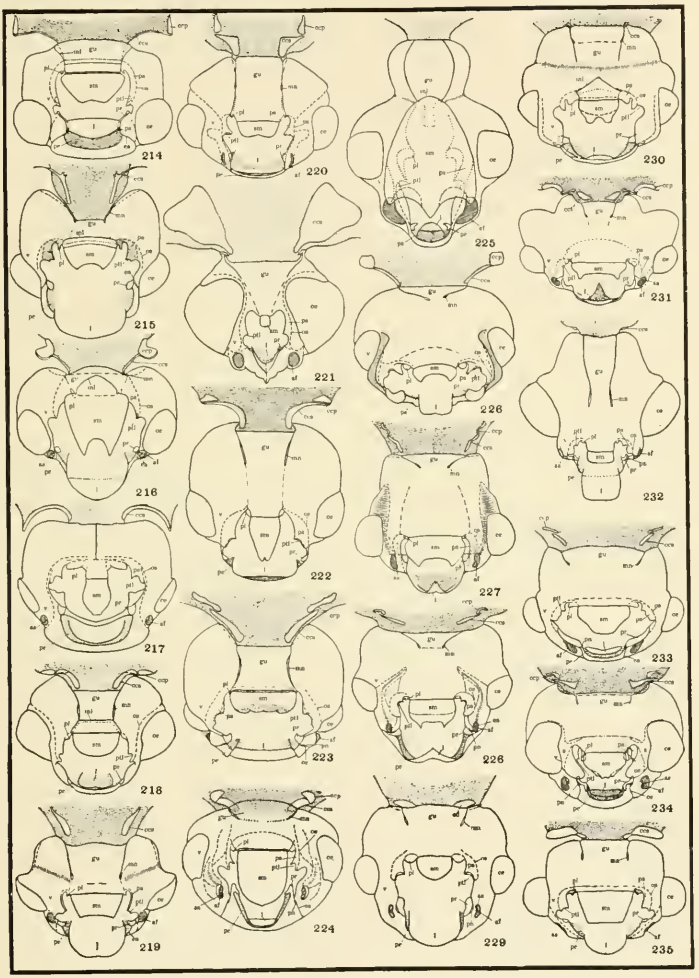
PLATE XI

EXPLANATION OF PLATE XI

VENTRAL ASPECT OF THE HEAD

Fig. 214. *Helichus striatus.*
Fig. 215. *Stenelmis sinuata.*
Fig. 216. *Heterocerus undatus.*
Fig. 217. *Georyssus californicus.*
Fig. 218. *Eurypogon niger.*
Fig. 219. *Eucinetus morio.*
Fig. 220. *Cyphon ruficollis.*
Fig. 221. *Chelonarium errans.*
Fig. 222. *Dermestes lardarius.*
Fig. 223. *Byrrhus americanus.*
Fig. 224. *Nosodendron unicolor.*
Fig. 225. *Rhysodes americanus.*
Fig. 226. *Tenebroides sinuatus.*
Fig. 227. *Phenolia grossa.*
Fig. 228. *Glischrochilus fasciatus.*
Fig. 229. *Rhizophagus bipunctatus.*
Fig. 230. *Phyconomus marinus.*
Fig. 231. *Cucujus clavipes.*
Fig. 232. *Hemipeplus marginipennis.*
Fig. 233. *Languria mozardi.*
Fig. 234. *Megalodacne fasciata.*
Fig. 235. *Derodontus maculatus.*

aa	antacoila	*od*	odontoidea
af	antafossa	*os*	occipital suture
ccp	cervepimeron	*pa*	postgena
ccs	cervepisternum	*pe*	preclypeus
cct	cervisternum	*pl*	paracoila
ce	compound eye	*pn*	pretentorina
ea	epicranial arm	*pr*	precoila
gu	gula	*ptl*	postcoila
inl	line of invagination	*sm*	submentum
l	labrum	*v*	vertex
mn	metatentorina		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XI

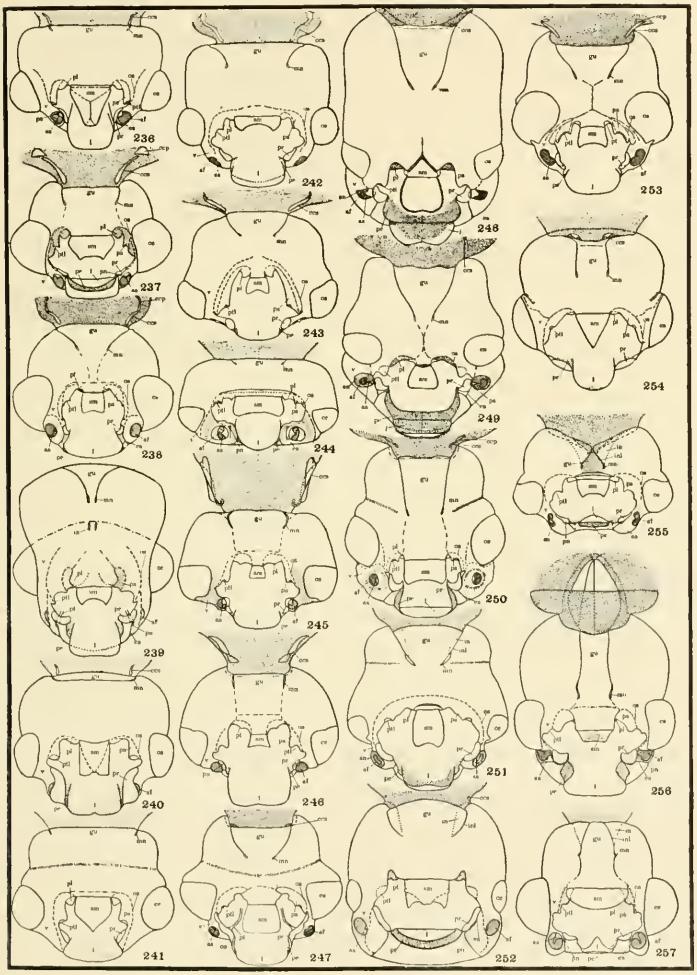
PLATE XII

EXPLANATION OF PLATE XII

VENTRAL ASPECT OF THE HEAD

Fig. 236. *Anchicera ephippiata.*
Fig. 237. *Byturus unicolor.*
Fig. 238. *Mycetophagus punctatus.*
Fig. 239. *Bothrideres geminatus.*
Fig. 240. *Philothermus glabriculus.*
Fig. 241. *Melanophthalma cavicollis.*
Fig. 242. *Phymaphora pulchella.*
Fig. 243. *Endomychus biguttatus.*
Fig. 244. *Phalacrus politus.*
Fig. 245. *Hippodamia convergens.*
Fig. 246. *Adalia bipunctata.*
Fig. 247. *Pseudocistela brevis.*
Fig. 248. *Alobates pennsylvanica.*
Fig. 249. *Tenebrio molitor.*
Fig. 250. *Boros unicolor.*
Fig. 251. *Arthromacra aenea.*
Fig. 252. *Hyporphagus* sp.
Fig. 253. *Penthe obliquata.*
Fig. 254. *Plinus brunneus.*
Fig. 255. *Sitodrepa panicea.*
Fig. 256. *Bostrichus bicornis.*
Fig. 257. *Lyctus planicollis.*

aa	antacoila	*mn*	metatentorina
af	antafossa	*os*	occipital suture
an	antacoria	*pa*	postgena
ccp	cervepimeron	*pe*	preclypeus
ccs	cervepisternum	*pl*	paracoila
ce	compound eye	*pn*	pretentorina
ea	epicranial arm	*pr*	precoila
gu	gula	*pt*	pretentorium
in	invagination	*ptl*	postcoila
inl	line of invagination	*sm*	submentum
l	labrum	*v*	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XII

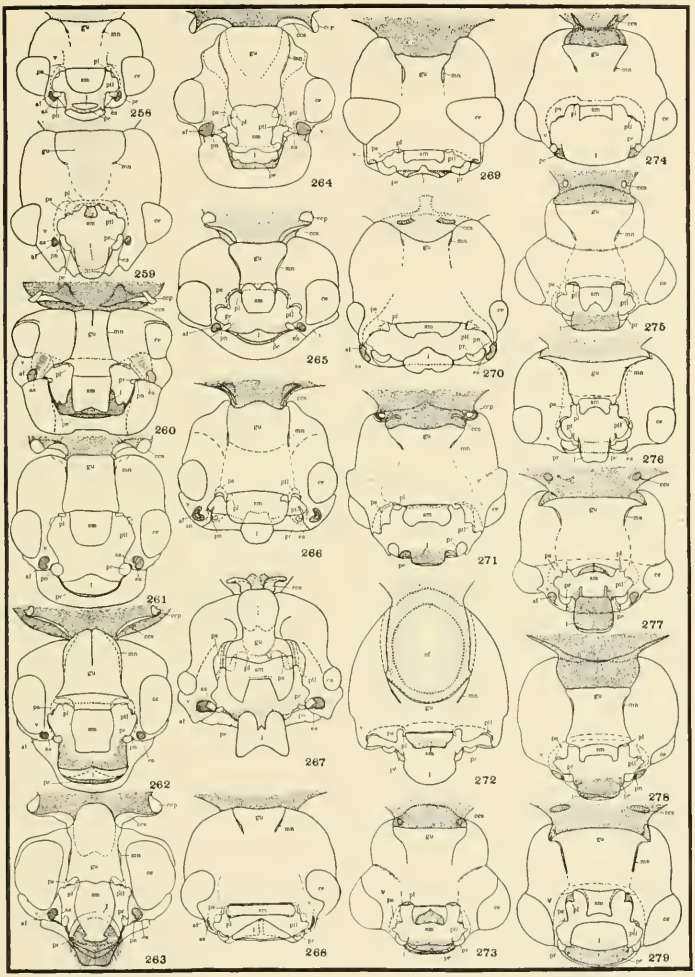
PLATE XIII

EXPLANATION OF PLATE XIII

VENTRAL ASPECT OF THE HEAD

Fig. 258. *Sphindus americanus.*
Fig. 259. *Plesiocis cribrum.*
Fig. 260. *Aphodius fimetarius.*
Fig. 261. *Dichelonyx elongata.*
Fig. 262. *Pelidnota punctata.*
Fig. 263. *Strategus julianus.*
Fig. 264. *Osmoderma eremicola.*
Fig. 265. *Trox suberosus.*
Fig. 266. *Pseudolucanus capreolus.*
Fig. 267. *Passalus cornutus.*
Fig. 268. *Parandra brunnea.*
Fig. 269. *Derobrachus brunneus.*
Fig. 270. *Spondylis buprestoides.*
Fig. 271. *Glycobius speciosus.*
Fig. 272. *Tetraopes tetrophthalmus.*
Fig. 273. *Donacia piscatrix.*
Fig. 274. *Syneta ferruginea.*
Fig. 275. *Criocerus asparagi.*
Fig. 276. *Cryptocephalus quadruplex.*
Fig. 277. *Chrysochus auratus.*
Fig. 278. *Leptinotarsa decemlineata.*
Fig. 279. *Diabrotica 12-punctata.*

aa	antacoila	*of*	occipital foramen
af	antafossa	*pa*	postgena
an	antacoria	*pe*	preclypeus
ccp	cervepimeron	*pl*	paracoila
ccs	cervepisternum	*pn*	pretentorina
ce	compound eye	*pr*	precoila
ea	epicranial arm	*pt*	pretentorium
gu	gula	*ptl*	postcoila
l	labrum	*sm*	submentum
mn	metatentorina	*v*	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XIII

PLATE XIV

EXPLANATION OF PLATE XIV

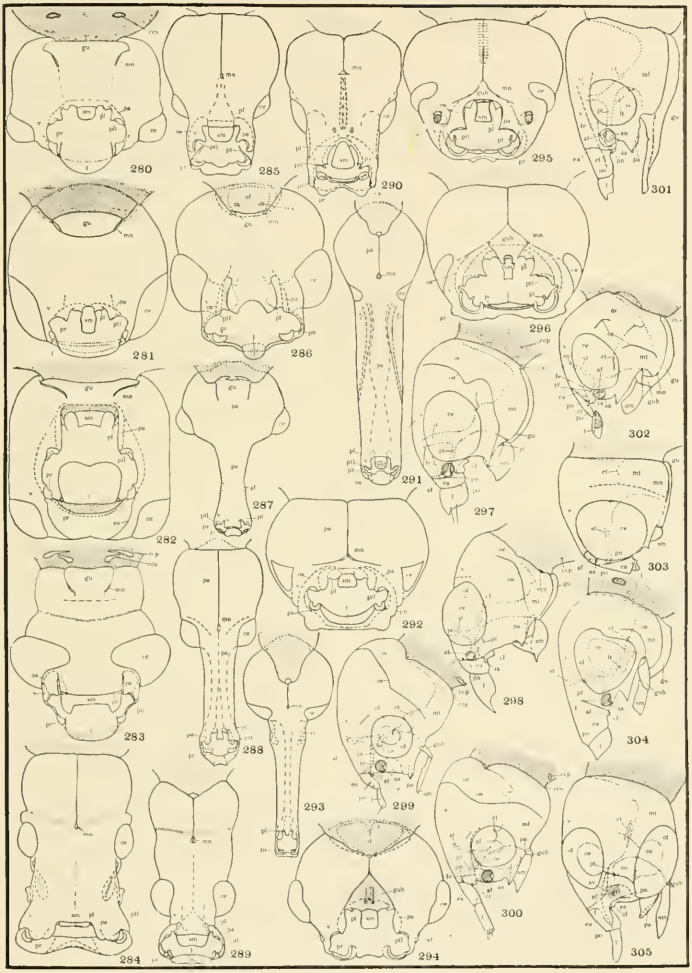
VENTRAL ASPECT OF THE HEAD

Fig. 280. *Blepharida rhois.*
Fig. 281. *Anoplitis gracilis.*
Fig. 282. *Chelymorpha argus.*
Fig. 283. *Pachymerus gleditsiae.*
Fig. 284. *Eupsalis minuta.*
Fig. 285. *Ithycerus noveboracensis.*
Fig. 286. *Eurymycter fasciatus.*
Fig. 287. *Rhinomacer pilosus.*
Fig. 288. *Rhynchites bicolor.*
Fig. 289. *Attelabus analis.*
Fig. 290. *Epicaerus imbricatus.*
Fig. 291. *Lixus fimbriolatus.*
Fig. 292. *Thecesternus humeralis.*
Fig. 293. *Sphenophorus aequalis.*
Fig. 294. *Platypus flavicornis.*
Fig. 295. *Scolytus quadrispinosus.*
Fig. 296. *Dendroctonus valens.*

LATERAL ASPECT OF THE HEAD

Fig. 297. *Tetracha carolina.*
Fig. 298. *Cicindela formosa.*
Fig. 299. *Calosoma calidum.*
Fig. 300. *Harpalus erraticus.*
Fig. 301. *Amphizoa lecontei.*
Fig. 302. *Omophron americanum.*
Fig. 303. *Pelidytes 12-punctatus.*
Fig. 304. *Cybister fimbriolatus.*
Fig. 305. *Dineutes americanus.*

aa	antacoila	*mt*	metatentorium
af	antafossa	*oc*	occiput
an	antacoria	*ol*	oculata
ccp	cervepimeron	*os*	occipital suture
ccs	cervepisternum	*pa*	postgena
ce	compound eye	*pe*	preclypeus
cl	clypealia	*pl*	paracoila
ct	corpotentorium	*pn*	pretentorina
ea	epicranial arm	*po*	postclypeus
eo	exoculata	*pr*	precoila
f	front	*pt*	pretentorium
fe	frontal ridge	*ptl*	postcoila
gu	gula	*sm*	submentum
gub	gula bar	*sn*	supratentorina
l	labrum	*st*	supratentorium
lt	laminatentorium	*v*	vertex
mn	metatentorina		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XIV

PLATE XV

EXPLANATION OF PLATE XV

LATERAL ASPECT OF THE HEAD

Fig. 306. *Hydrsena marginicollis.*
Fig. 307. *Hydroscapha natans.*
Fig. 308. *Hydrous triangularis.*
Fig. 309. *Hydrophilus obtusatus.*
Fig. 310. *Platypsyllus castoris.*
Fig. 311. *Brathinus nitidus.*
Fig. 312. *Leptinus testaceus.*
Fig. 313. *Necrophorus carolinus.*
Fig. 314. *Clambus puberulus.*
Fig. 315. *Connophron fossiger.*
Fig. 316. *Molamba lunata.*
Fig. 317. *Sienus flavicornis.*
Fig. 318. *Gastrolobium bicolor.*
Fig. 319. *Creophilus villosus.*
Fig. 320. *Tachinus fimbriatus.*
Fig. 321. *Alecchara lata.*
Fig. 322. *Pilopius lacustris.*
Fig. 323. *Fustiger fuchsi.*
Fig. 324. *Limulodes paradoxus.*

ca	antacoila	*li*	laminatentorium
af	antafossa	*mn*	metatentorina
cep	cervepimeron	*mt*	metatentorium
ces	cervepisternum	*ol*	oculata
ce	compound eye	*pa*	postgena
ch	chitinized area	*pe*	preclypeus
cl	clypealia	*pl*	paracoila
ct	corpotentorium	*pn*	pretentorina
ea	epicranial arm	*po*	postclypeus
f	front	*pr*	precoila
fe	frontal ridge	*pt*	pretentorium
gu	gula	*sm*	submentum
gub	gula bar	*st*	supratentorium
l	labrum	*v*	vertex

STICAL BY HEAD-CAPSULE OF COLEOPTERA PLATE 2

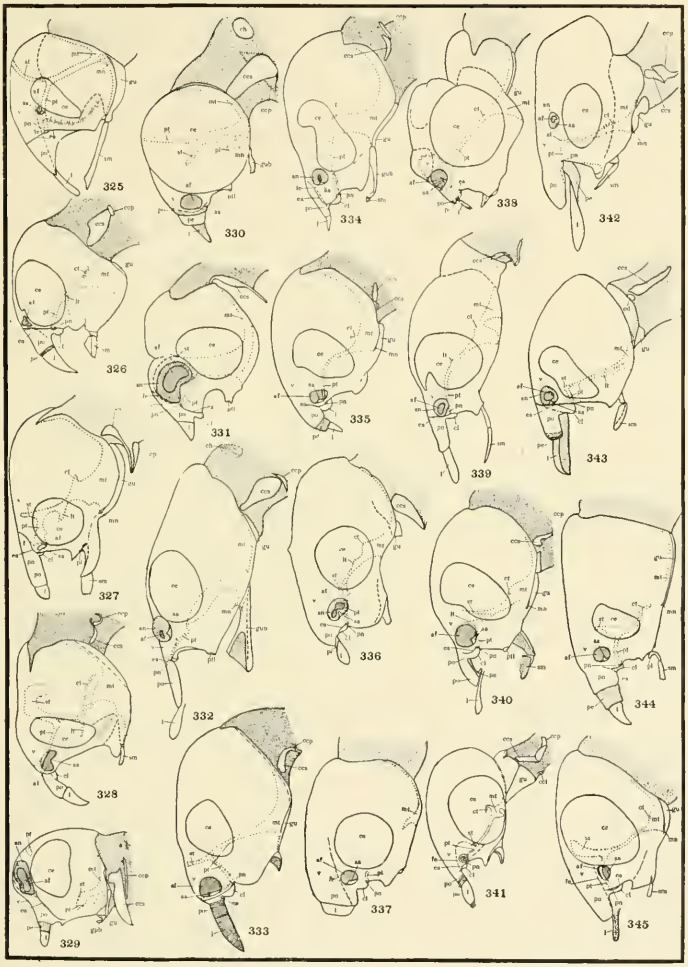
PLATE XVI

EXPLANATION OF PLATE XVI

LATERAL ASPECT OF THE HEAD

Fig. 325. *Sphaerius politus.*
Fig. 326. *Scaphidium quadriguttatum.*
Fig. 327. *Sphaerites glabratus.*
Fig. 328. *Hister memnonius.*
Fig. 329. *Calopteron terminale.*
Fig. 330. *Photinus pyralis.*
Fig. 331. *Phengodes plumosa.*
Fig. 332. *Chauliognathus pennsylvanicus.*
Fig. 333. *Collops nigriceps.*
Fig. 334. *Trichodes nutalli.*
Fig. 335. *Necrobia rufipes.*
Fig. 336. *Hylecoetus lugubris.*
Fig. 337. *Micromalthus debilis.*
Fig. 338. *Cupes concolor.*
Fig. 339. *Cephaloon lepturides.*
Fig. 340. *Nacerda melanura.*
Fig. 341. *Tomoxia bidentata.*
Fig. 342. *Macrosiagon dimidiatum.*
Fig. 343. *Epicauta marginata.*
Fig. 344. *Eurystethus debilis.*
Fig. 345. *Othinus* sp.

aa	antacoila	*gub*	gula bar
af	antafossa	*l*	labrum
an	antacoria	*lt*	laminatentorium
ccp	cervepimeron	*mn*	metatentorina
ccs	cervepisternum	*mt*	metatentorium
cct	cervesternum	*pe*	preclypeus
ce	compound eye	*pl*	paracoila
ch	chitinized area	*pn*	pretentorina
cl	clypealia	*po*	postclypeus
ct	corpotentorium	*pt*	pretentorium
ea	epicranial arm	*ptl*	postcoila
f	front	*sm*	submentum
fe	frontal ridge	*st*	supratentorium
gu	gula	*v*	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XVI

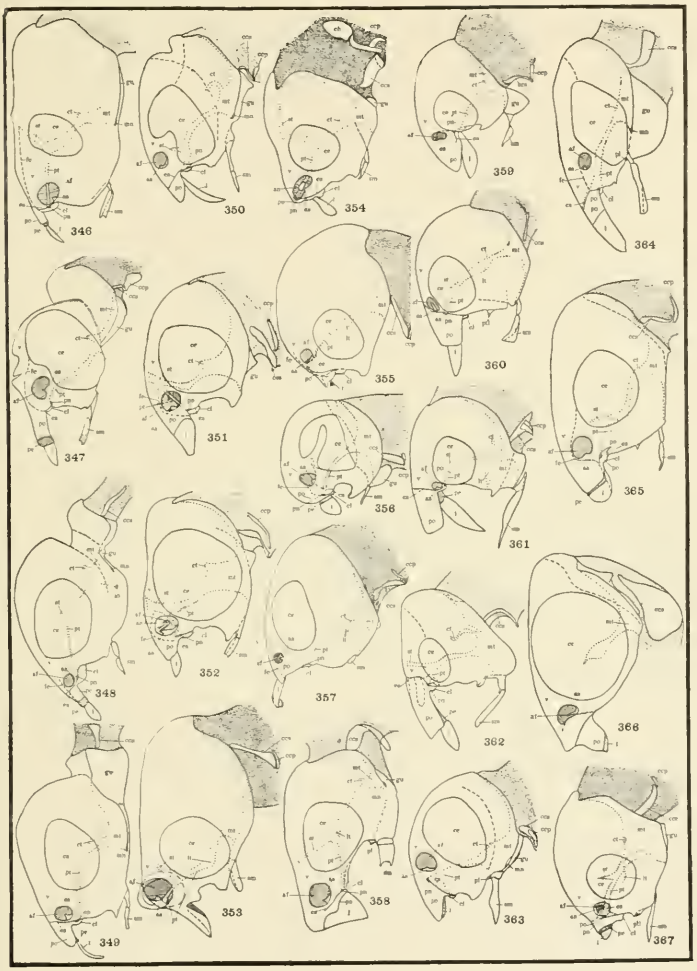
PLATE XVII

EXPLANATION OF PLATE XVII

LATERAL ASPECT OF THE HEAD

Fig. 346. *Pytho planus.*
Fig. 347. *Neopyrochroa flabellata.*
Fig. 348. *Macratria murina.*
Fig. 349. *Notoxus anchora.*
Fig. 350. *Zonantes fasciatus.*
Fig. 351. *Cebrio bicolor.*
Fig. 352. *Euthysanius lautus.*
Fig. 353. *Sandalus niger.*
Fig. 354. *Alaus oculatus.*
Fig. 355. *Isorhipis ruficornis.*
Fig. 356. *Throscus chevrolati.*
Fig. 357. *Chalcophora virginiensis.*
Fig. 358. *Psephenus lecontei.*
Fig. 359. *Helichus striatus.*
Fig. 360. *Stenelmis sinuata.*
Fig. 361. *Heterocerus undatus.*
Fig. 362. *Georyssus californicus.*
Fig. 363. *Eurypogon niger.*
Fig. 364. *Eucinetus morio.*
Fig. 365. *Cyphon ruficollis.*
Fig. 366. *Chelonarium errans.*
Fig. 367. *Dermestes lardarius.*

aa	antacoila
af	antafossa
an	antacoria
ccp	cervepimeron
ccs	cervepisternum
ce	compound eye
ch	chitinized area
cl	clypealia
ct	corpotentorium
ea	epicranial arm
fe	frontal ridge
gu	gula
in	invagination
l	labrum
lt	laminatentorium
mn	metatentorina
mt	metatentorium
pe	preclypeus
pl	paracoila
pn	pretentorina
po	postclypeus
pt	pretentorium
ptl	postcoila
sm	submentum
st	supratentorium
v	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XVII

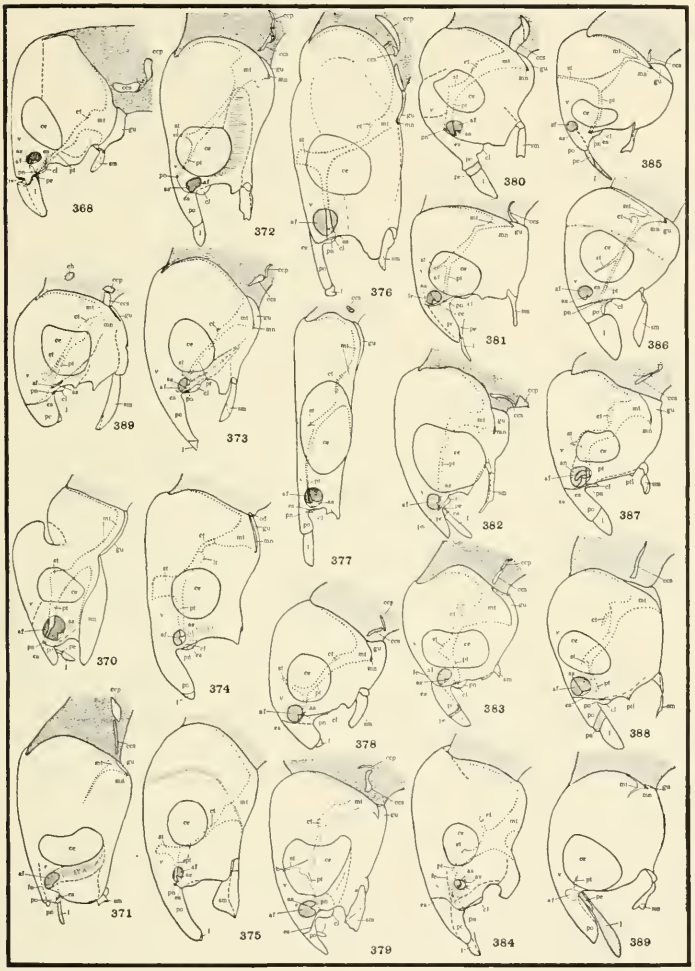
PLATE XVIII

EXPLANATION OF PLATE XVIII

LATERAL ASPECT OF THE HEAD

Fig. 368. *Byrrhus americanus.*
Fig. 369. *Nosodendron unicolor.*
Fig. 370. *Rhysodes americanus.*
Fig. 371. *Tenebroides sinuatus.*
Fig. 372. *Phenolia grossa.*
Fig. 373. *Glischrochilus fasciatus.*
Fig. 374. *Rhizophagus bipunctatus.*
Fig. 375. *Phyconomus marinus.*
Fig. 376. *Cucujus clavipes.*
Fig. 377. *Hemipeplus marginipennis.*
Fig. 378. *Languria mozardi.*
Fig. 379. *Megalodacne fasciata.*
Fig. 380. *Derodontus maculatus.*
Fig. 381. *Anchicera ephippiata.*
Fig. 382. *Byturus unicolor.*
Fig. 383. *Mycetophagus punctatus.*
Fig. 384. *Bothrideres geminatus.*
Fig. 385. *Philothermus glabriculus.*
Fig. 386. *Melanophthalma cavicollis.*
Fig. 387. *Phymaphora pulchella.*
Fig. 388. *Endomychus biguttatus.*
Fig. 389. *Phalacrus politus.*

aa	antacoila	*lt*	laminatentorium
af	antafossa	*mn*	metatentorina
an	antacoria	*mt*	metatentorium
av	antacava	*od*	odontoidea
ccp	cervepimeron	*pe*	preclypeus
ccs	cervepisternum	*pl*	paracoila
ce	compound eye	*pn*	pretentorina
ch	chitinized area	*po*	postclypeus
cl	clypealia	*pt*	pretentorium
ct	corpotentorium	*ptl*	postcoila
ca	epicranial arm	*sm*	submentum
fe	frontal ridge	*st*	supratentorium
gu	gula	*v*	vertex
l	labrum		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XVIII

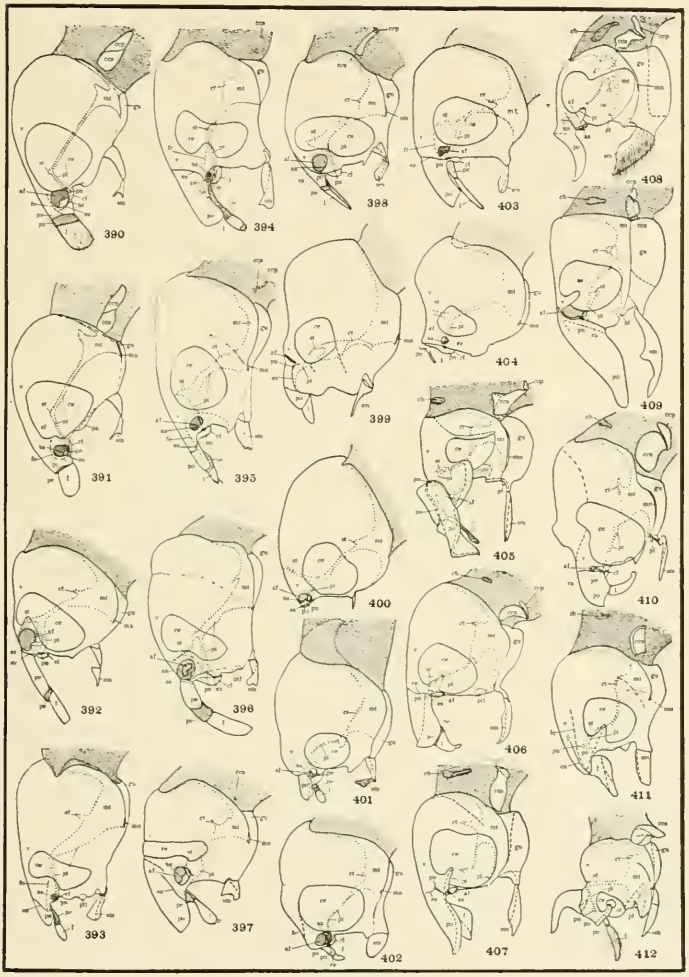
PLATE XIX

EXPLANATION OF PLATE XIX

LATERAL ASPECT OF THE HEAD

Fig. 390. *Hippodamia convergens.*
Fig. 391. *Adolia bipunctatus.*
Fig. 392. *Pseudocistela brevis.*
Fig. 393. *Alobates pennsylvanica.*
Fig. 394. *Tenebrio molitor.*
Fig. 395. *Boros unicolor.*
Fig. 396. *Arthromacra aenea.*
Fig. 397. *Hyporphagus* sp.
Fig. 398. *Penthe obliquata.*
Fig. 399. *Ptinus brunneus.*
Fig. 400. *Sitodrepa panicea.*
Fig. 401. *Bostrichus bicornis.*
Fig. 402. *Lyctus planicollis.*
Fig. 403. *Sphindus americanus.*
Fig. 404. *Plesiocis cribrum.*
Fig. 405. *Aphodius fimetarius.*
Fig. 406. *Dichelonyx elongata.*
Fig. 407. *Pelidnota punctata.*
Fig. 408. *Strategus julianus.*
Fig. 409. *Osmoderma eremicolla.*
Fig. 410. *Trox suberosus.*
Fig. 411. *Pseudolucanus capreolus.*
Fig. 412. *Passalus cornutus.*

aa	antacoila	*l*	labrum
af	antafossa	*mn*	metatentorina
an	antacoria	*mt*	metatentorium
ccp	cervepimeron	*ol*	oculata
ccs	cervepisternum	*pe*	preclypeus
ce	compound eye	*pl*	paracoila
ch	chitinized area	*pn*	pretentorina
cl	clypealia	*po*	postclypeus
ct	corpotentorium	*pt*	pretentorium
ea	epicranial arm	*sm*	submentum
fe	frontal ridge	*st*	supratentorium
gu	gula	*v*	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XIX

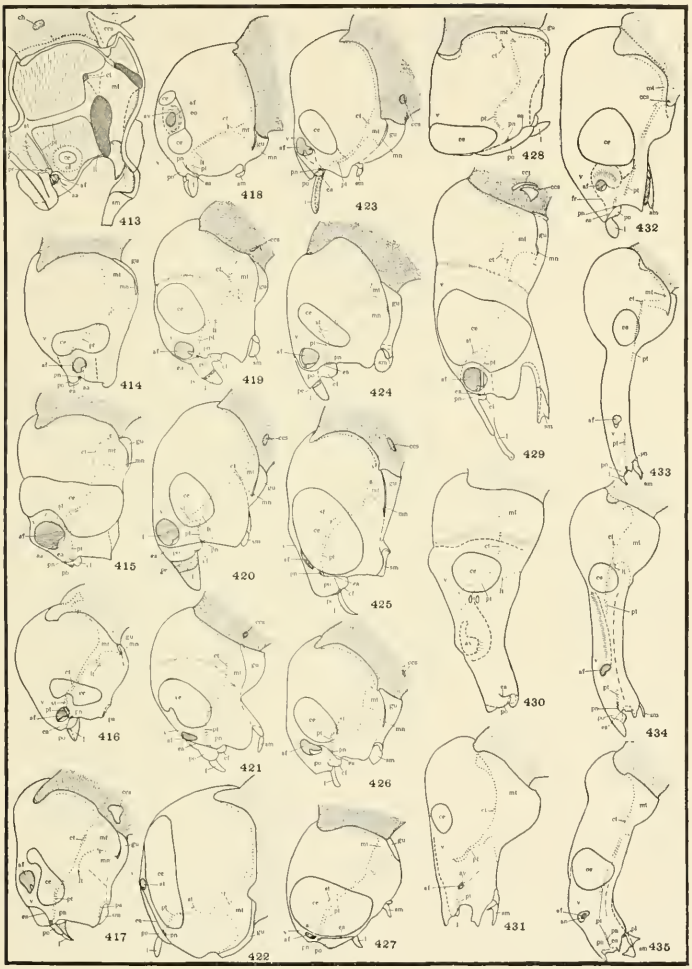
PLATE XX

EXPLANATION OF PLATE XX

LATERAL ASPECT OF THE HEAD

Fig. 413. *Passalus cornutus.*
Fig. 414. *Parandra brunnea.*
Fig. 415. *Derobrachus brunneus.*
Fig. 416. *Spondylis buprestoides.*
Fig. 417. *Glycobius speciosus.*
Fig. 418. *Tetraopes tetraophthalmus.*
Fig. 419. *Donacia piscatrix.*
Fig. 420. *Syneta ferruginea.*
Fig. 421. *Criocerus asparagi.*
Fig. 422. *Cryptocephalus quadruplex.*
Fig. 423. *Chrysochus auratus.*
Fig. 424. *Leptinotarsa decemlineata*
Fig. 425. *Diabrotica 12-punctata.*
Fig. 426. *Blepharida rhois.*
Fig. 427. *Anoplitis gracilis.*
Fig. 428. *Chelymorpha argus.*
Fig. 429. *Pachymerus gleditsiae.*
Fig. 430. *Eupsalis minuta.*
Fig. 431. *Ithycerus noveboracensis.*
Fig. 432. *Eurymycter fasciatus.*
Fig. 433. *Rhinomacer pilosus.*
Fig. 434. *Rhynchites bicolor.*
Fig. 435. *Attelabus analis.*

aa	antacoila	*lt*	laminatentorium
af	antafossa	*mn*	metatentorina
an	antacoria	*mt*	metatentorium
av	antacava	*ol*	oculata
ccp	cervepimeron	*pa*	postgena
ccs	cervepisternum	*pe*	preclypeus
ce	compound eye	*pl*	paracoila
ch	chitinized area	*pn*	pretentorina
cl	clypealia	*po*	postclypeus
ct	corpotentorium	*pr*	precoila
ea	epicranial arm	*pt*	pretentorium
fe	frontal ridge	*sm*	submentum
gu	gula	*st*	supratentorium
l	labrum	*v*	vertex



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XX

PLATE XXI

EXPLANATION OF PLATE XXI

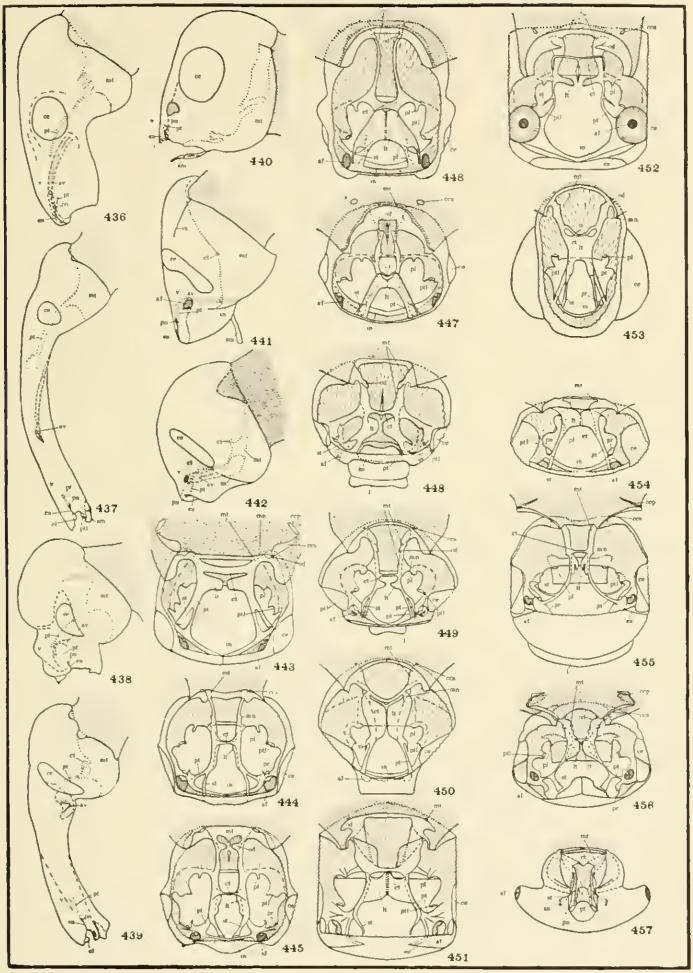
LATERAL ASPECT OF THE HEAD

Fig. 436. *Epicaerus imbricatus.*
Fig. 437. *Lixus fimbriolatus.*
Fig. 438. *Thecesternus humeralis.*
Fig. 439. *Sphenophorus aequalis.*
Fig. 440. *Platypus flavicornis.*
Fig. 441. *Scolytus quadrispinosus.*
Fig. 442. *Dendroctonus valens.*

ENDOSKELETON OF THE HEAD

Fig. 443. Hypothetical type.
Fig. 444. *Tetracha carolina.*
Fig. 445. *Cicindela formosa.*
Fig. 446. *Calosoma calidum.*
Fig. 447. *Harpalus erraticus.*
Fig. 448. *Amphizoa lecontei.*
Fig. 449. *Omophron americanum.*
Fig. 450. *Peltodytes 12-punctata.*
Fig. 451. *Cybister fimbriolatus.*
Fig. 452. *Dineutes americanus.*
Fig. 453. *Hydracna marginicollis.*
Fig. 454. *Hydroscapha natans.*
Fig. 455. *Hydrous triangularis.*
Fig. 456. *Hydrophilus obtusatus.*
Fig. 457. *Platypsyllus castoris.*

af	antafossa	*mn*	metatentorina
av	antacava	*mt*	metatentorium
ccp	cervepimeron	*od*	odontoidea
ccs	cervepisternum	*pl*	paracoila
ce	compound eye	*pn*	pretentorina
cl	clypealia	*pr*	precoila
ct	corpotentorium	*pt*	pretentorium
ea	epicranial arm	*ptl*	postcoila
in	invagination	*sm*	submentum
l	labrum	*sn*	supratentorina
lt	laminatentorium	*st*	supratentorium



STICKNEY — HEAD-CAPSULE OF COLEOPTERA PLATE XXI

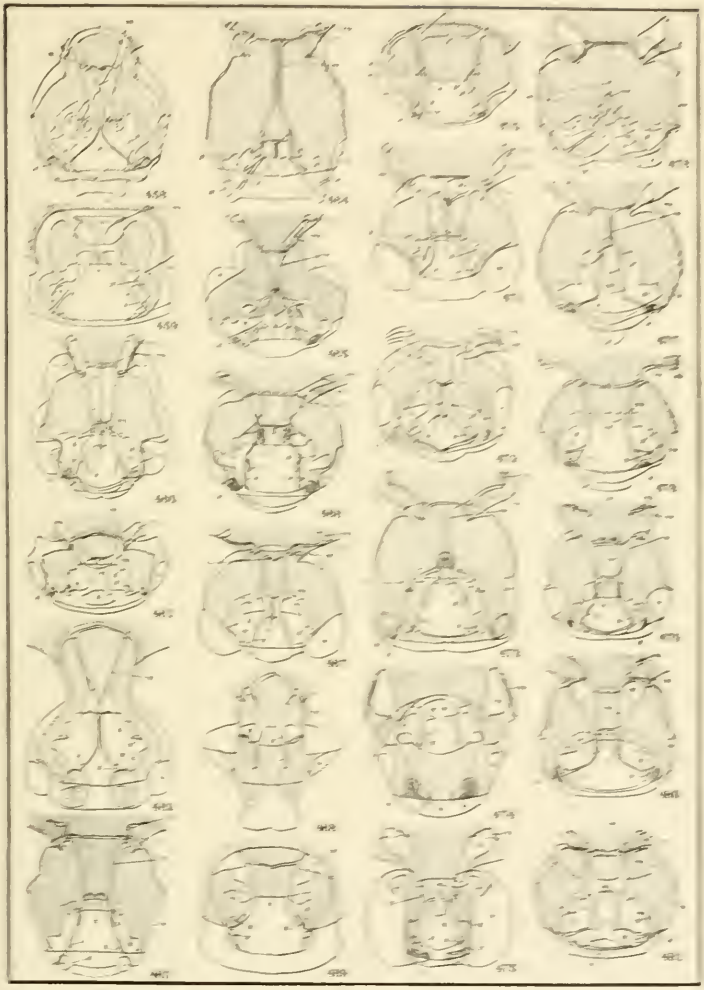
PLATE XXII

EXPLANATION OF PLATE XXII

DISSECTION OF THE HEAD

Fig. 455. *Protenor vitalis*.
Fig. 456. *Lygaeus kalmii*.
Fig. 457. *Nabis subcoleoptratus*.
Fig. 458. *Corimelaena pulicaria*.
Fig. 459. *Coreopsis lucida*.
Fig. 460. *Alydus pilosulus*.
Fig. 461. *Leptocoris trivittatus*.
Fig. 462. *Euschistus tristigmus*.
Fig. 463. *Podisus placidus*.
Fig. 464. *Sinea diadema*.
Fig. 465. *Zelus luridus*.
Fig. 466. *Phymata wolffii*.
Fig. 467. *Gerris remigis*.
Fig. 468. *Notonecta undulata*.
Fig. 469. *Corixa interrupta*.
Fig. 470. *Belostoma flumineum*.
Fig. 471. *Nepa apiculata*.
Fig. 472. *Ranatra fusca*.
Fig. 473. *Pelocoris femoratus*.
Fig. 474. *Rhagovelia obesa*.
Fig. 475. *Gerris marginatus*.
Fig. 476. *Hydrometra martini*.
Fig. 477. *Velia rivularis*.
Fig. 478. *Trichocorixa sexcincta*.
Fig. 479. *Notonecta undulata*.
Fig. 480. *Ranatra fusca*.

a.	antennae
ac.	acetabulum
an.	anus
c.	coxa
cl.	clypeus
cp.	compound eye
e.	epicranium
f.	femur
fm.	foramen magnum
g.	gena
gf.	groove for beak
l.	labium
la.	labrum
m.	mandibles
mc.	metacoxa
mf.	metafemur
mt.	metatibia
o.	ocellus
p.	prothorax
pc.	procoxa
pf.	profemur
pt.	protibia
s.	sternum
sc.	scutellum
t.	tibia



TURNER HEAD-CAPSULE OF COLEOPTERA PLATE XXIII

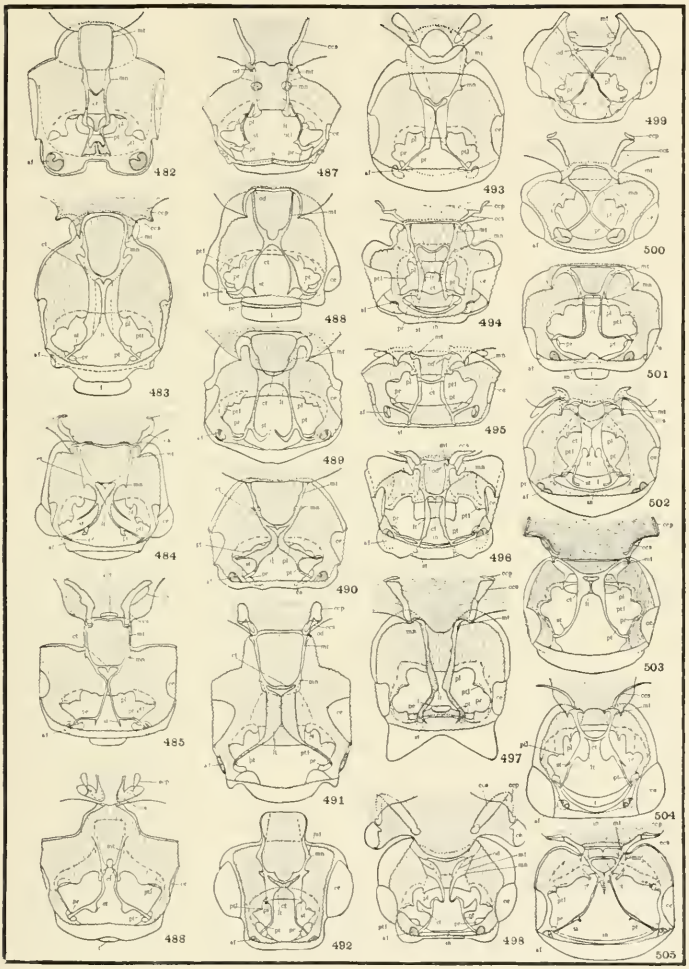
PLATE XXIII

EXPLANATION OF PLATE XXIII

ENDOSKELETON OF THE HEAD

Fig. 482. *Cupes concolor.*
Fig. 483. *Cephaloon lepturides.*
Fig. 484. *Nacerda melanura.*
Fig. 485. *Tomoxia bidentata.*
Fig. 486. *Macrosiagon dimidiatum.*
Fig. 487. *Epicauta marginata.*
Fig. 488. *Eurystethus debilis.*
Fig. 489. *Othnius* sp.
Fig. 490. *Pytho planus.*
Fig. 491. *Neopyrochroa flabellata.*
Fig. 492. *Macratria murina.*
Fig. 493. *Notoxus anchora.*
Fig. 494. *Zonantes fasciatus.*
Fig. 495. *Cebrio bicolor.*
Fig. 496. *Euthysanius lautus.*
Fig. 497. *Sandalus niger.*
Fig. 498. *Alaus oculatus.*
Fig. 499. *Isorhipis ruficornis.*
Fig. 500. *Throscus chevrolati.*
Fig. 501. *Chalcophora virginiensis.*
Fig. 502. *Psephenus lecontei.*
Fig. 503. *Helichus striatus.*
Fig. 504. *Stenelmis sinuata.*
Fig. 505. *Heterocerus undatus.*

af	antafossa	*lt*	laminatentorium
ccp	cervepimeron	*mn*	metatentorina
ccs	cervepisternum	*mt*	metatentorium
cct	cervesternum	*od*	odontoidea
ce	compound eye	*pl*	paracoila
ch	chitinized area	*pr*	precoila
et	corpotentorium	*pt*	pretentorium
ea	epicranial arm	*ptl*	postcoila
in	invagination	*st*	supratentorium
l	labrum		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XXIII

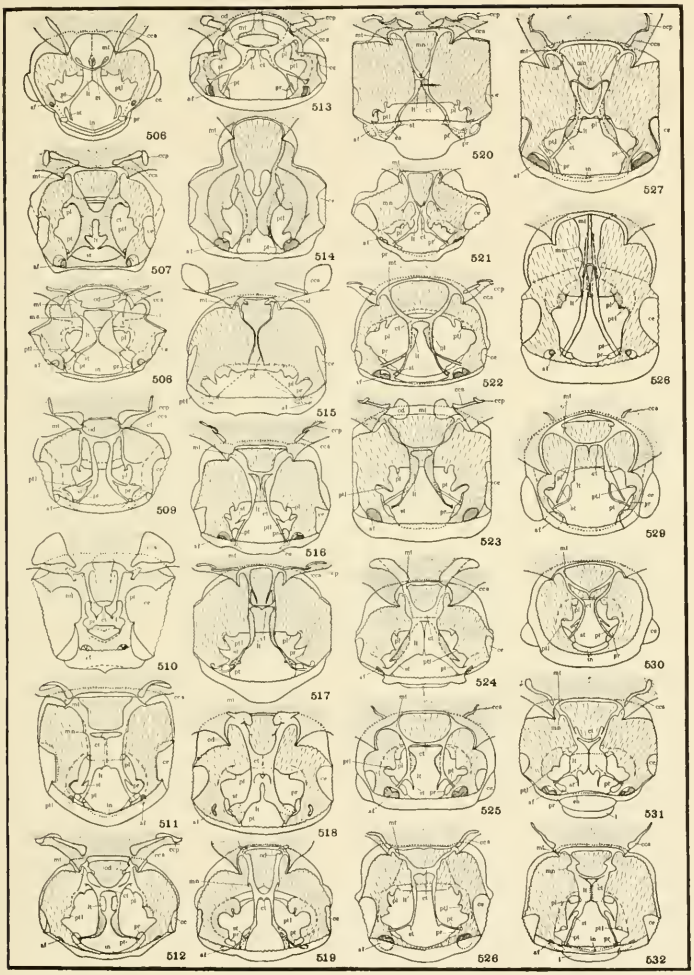
PLATE XXIV

EXPLANATION OF PLATE XXIV

ENDOSKELETON OF THE HEAD

Fig. 506. *Georyssus californicus.*
Fig. 507. *Eurypogon niger.*
Fig. 508. *Eucinetus morio.*
Fig. 509. *Cyphon ruficollis.*
Fig. 510. *Chelonarium errans.*
Fig. 511. *Dermestes lardarius.*
Fig. 512. *Byrrhus americanus.*
Fig. 513. *Nosodendron unicolor.*
Fig. 514. *Rhysodes americanus.*
Fig. 515. *Tenebroides sinuatus.*
Fig. 516. *Phenolia grossa.*
Fig. 517. *Glischrochilus fasciatus.*
Fig. 518. *Rhizophagus bipunctatus.*
Fig. 519. *Phyconomus marinus.*
Fig. 520. *Cucujus clavipes.*
Fig. 521. *Hemipeplus marginipennis.*
Fig. 522. *Languria mozardi.*
Fig. 523. *Megalodacne fasciata.*
Fig. 524. *Derodontus maculatus.*
Fig. 525. *Anchicera ephippiata.*
Fig. 526. *Byturus unicolor.*
Fig. 527. *Mycetophagus punctatus.*
Fig. 528. *Bothrideres geminatus.*
Fig. 529. *Philothermus glabriculus.*
Fig. 530. *Melanophthalma cavicollis.*
Fig. 531. *Phymaphora pulchella.*
Fig. 532. *Endomychus biguttatus.*

af	antafossa	*mn*	metatentorina
ccp	cervepimeron	*mt*	metatentorium
ccs	cervepisternum	*od*	odontoidea
cct	cervisternum	*pl*	paracoila
ce	compound eye	*pr*	precoila
ct	corpotentorium	*pt*	pretentorium
in	invagination	*ptl*	postcoila
l	labrum	*st*	supratentorium
lt	laminatentorium		



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XXIV

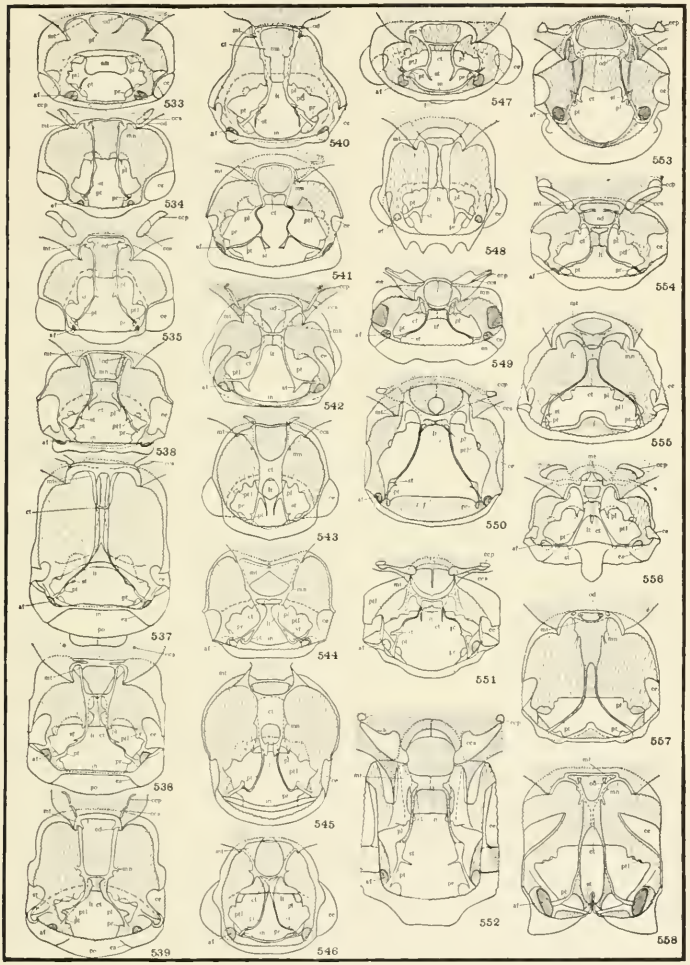
PLATE XXV

EXPLANATION OF PLATE XXV

ENDOSKELETON OF THE HEAD

Fig. 533. *Phalacrus politus.*
Fig. 534. *Hippodamia convergens.*
Fig. 535. *Adalia bipunctata.*
Fig. 536. *Pseudocistela brevis.*
Fig. 537. *Alobates pennsylvanica.*
Fig. 538. *Tenebrio molitor.*
Fig. 539. *Boros unicolor.*
Fig. 540. *Arthromacra aenea.*
Fig. 541. *Hyporphagus* sp.
Fig. 542. *Penthe obliquata.*
Fig. 543. *Ptinus brunneus.*
Fig. 544. *Sitodrepa panicea.*
Fig. 545. *Bostrichus bicornis.*
Fig. 546. *Lyctus planicollis.*
Fig. 547. *Sphindus americanus.*
Fig. 548. *Plesiocis cribrum.*
Fig. 549. *Aphodius fimetarius.*
Fig. 550. *Dichelonyx elongata.*
Fig. 551. *Pelidnota punctata.*
Fig. 552. *Strategus julianus.*
Fig. 553. *Osmoderma eremicola.*
Fig. 554. *Trox suberosus.*
Fig. 555. *Pseudolucanus capreolus.*
Fig. 556. *Passalus cornutus.*
Fig. 557. *Parandra brunnea.*
Fig. 558. *Derobrachus brunneus.*

af	antafossa	*mn*	metatentorina
ccp	cervepimeron	*mt*	metatentorium
ccs	cervepisternum	*od*	odontoidea
cct	cervisternum	*pl*	paracoila
ce	compound eye	*po*	postclypeus
ct	corpotentorium	*pr*	precoila
ea	epicranial arm	*pt*	pretentorium
in	invagination	*ptl*	postcoila
l	labrum	*sm*	submentum
lt	laminatentorium	*st*	supratentorium



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XXV

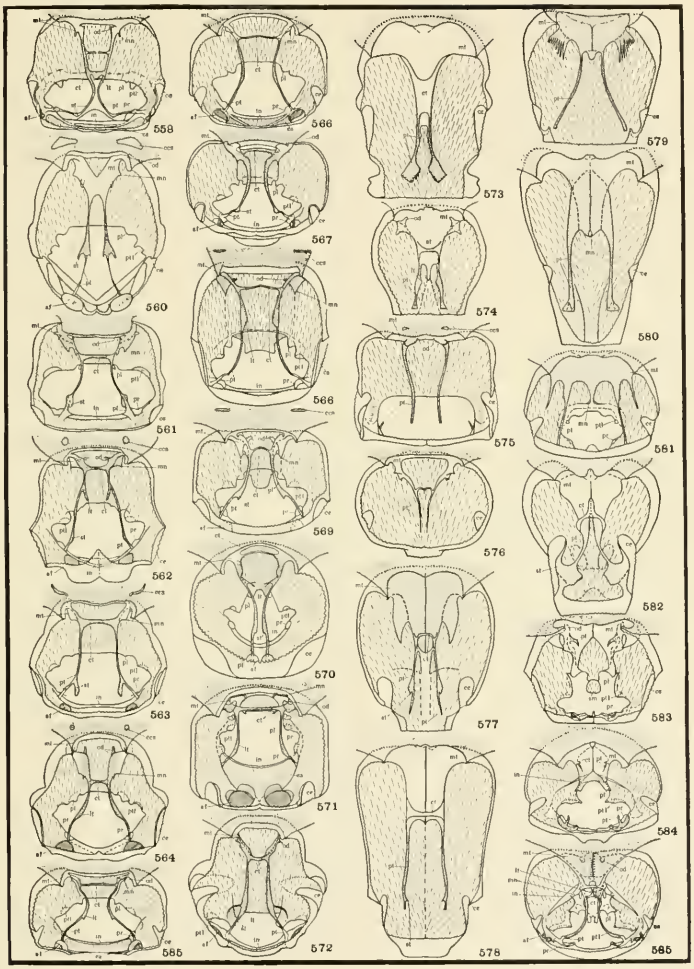
PLATE XXVI

EXPLANATION OF PLATE XXVI

ENDOSKELETON OF THE HEAD

Fig. 559. *Spondylis buprestoides.*
Fig. 560. *Glycobius speciosus.*
Fig. 561. *Tetraopes tetraophthalmus.*
Fig. 562. *Donacia piscatrix.*
Fig. 563. *Syneta ferruginea.*
Fig. 564. *Criocerus asparagi.*
Fig. 565. *Cryptocephalus quadruplex.*
Fig. 566. *Chrysochus auratus.*
Fig. 567. *Leptinotarsa decemlineata.*
Fig. 568. *Diabrotica 12-punctata.*
Fig. 569. *Blepharida rhois.*
Fig. 570. *Anoplitis gracilis.*
Fig. 571. *Chelymorpha argus.*
Fig. 572. *Pachymerus gleditsiae.*
Fig. 573. *Eupsalis minuta.*
Fig. 574. *Ithycerus noveboracensis.*
Fig. 575. *Eurymycter fasciatus.*
Fig. 576. *Rhinomacer pilosus.*
Fig. 577. *Rhynchites bicolor.*
Fig. 578. *Attelabus analis.*
Fig. 579. *Epicaerus imbricatus.*
Fig. 580. *Lixus fimbriolatus.*
Fig. 581. *Thecesternus humeralis.*
Fig. 582. *Sphenophorus aequalis.*
Fig. 583. *Platypus flavicornis.*
Fig. 584. *Scolytus quadrispinosus.*
Fig. 585. *Dendroctonus valens.*

af antafossa
ces cervepisternum
ce compound eye
ct corpotentorium
ea epicranial arm
in invagination
lt laminatentorium
mn metatentorina
mt metatentorium
od odontoidea
pl paracoila
pr precoila
pt pretentorium
ptl postcoila
st supratentorium



STICKNEY HEAD-CAPSULE OF COLEOPTERA PLATE XXVI

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COMPARATIVE STUDIES ON CERTAIN FEATURES OF NEMATODES AND THEIR SIGNIFICANCE

WITH FOUR PLATES AND SIX TEXT FIGURES

BY

DUNCAN CHARTERIS HETHERINGTON

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward
No. 223

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1922

TABLE OF CONTENTS

Introduction 7
Some new methods of nematode technique 7
Symmetry and structure of the head region 13
General considerations 13
Type form of the primitive nematode 13
Alterations in bilaterality of primitive type 16
Primitive orientation of nematodes 16
Definition of the primitive nematode 18
Cephalic structure in free-living nematodes 20
Symmetrical type of the esophagus 20
Pharyngeal modifications 22
Oral structures among nematodes 24
The structurally simple form 24
The primitive form 24
Modifications by division and fusion of structural elements 25
Modifications by loss of parts 28
Considerations of symmetry in the head region 29
Primitive and fundamental symmetry 29
Radial symmetry 30
Disymmetry 30
Asymmetry 30
Cephalic structure in parasitic nematodes 31
Symmetrical type of the esophagus 31
Cephalic modifications and relation to habitat 31
Pharyngeal modifications 33
Oral structure and symmetry 33
Simple forms 33
Disymmetrical forms from three-lipped ones 34
Other disymmetrical forms simulating jaws 34
Variations arising from number of lips and capsules 35
Ciliation among nematodes 39
Former views and present data 39
Significance of ciliation 41
Discussion and Conclusions 42
List of free-living species cited 44
List of parasitic species mentioned 44
Bibliography 47
Explanation of Plates 56

INTRODUCTION

The members of the phylum Nematoda both the parasitic and free living forms are exceptionally interesting in view of the varieties of structure existing in the cephalic region and also in view of the changes in structural symmetry from the fundamental bilaterality to pseudo-radial symmetry, true radial symmetry, and asymmetry.

In the following pages the author has directed his attention to a comparative study of the symmetry and structural variety of the cephalic regions existing among the nematodes, parasitic and free living, endeavoring throughout to determine the most primitive cephalic plan from which the most complicated forms were derived and the order of this derivation. Furthermore, some new and valuable methods of nematode technique have been devised to lessen the tedium and numerous difficulties involved in preparing this material for microscopical examination either as sections or toto-mounts and in addition, the question of ciliation among nematodes is discussed and evidence presented for the undoubted existence of such structures.

This comparative study was undertaken at the suggestion of Dr. Henry B. Ward, to whom the author at this time wishes to express his sincere thanks, not only for his interest in this study, but also for permission to use his private literature files and material from his collection of unnamed parasites. Further thanks are due to the other members of the department also for their kindly help and criticism.

SOME NEW METHODS OF NEMATODE TECHNIQUE

The difficulties involved in the preparation of nematodes for microscopical examination either as totos or sections can be appreciated fully only by those who have made any attempts whatsoever in that direction. Perhaps this fact has been one contributing in no small degree to the scarcity of workers in the field as compared with other fields of zoology and has at the same time been responsible in a measure for the confusion of nematode literature on systematic relations through the piling up of countless, meager, stereotyped descriptions, many of them based only on external appearances, gross anatomical features, and measurements. Few comprehensive studies exist on the gross and histological anatomy or upon physiological systems of the legion of nematodes known, comparable to the works of Looss on the life history and anatomy of the hookworm or of Martini on *Oxyuris curvula*.

The main points of a simplified and rapid technique suitable for the microscopical preparation of the larger free living and parasitic nematodes may be found in an article by the author (Hetherington 1922), the essentials of which will be repeated here for convenience, with the addition of a few suggestions and comments.

The greatest obstacle to successful nematode preparation is the almost impenetrable cuticula in which the animal is encased, as it were, offering a splendid barrier to the entrance of the ordinary fixatives and clearing media, particularly the resinous ones in which one often desires to mount specimens.

During a series of experiments with various killing and dehydrating fluids it was noticed that little collapse and crumpling took place in fluids containing acids as lactic and acetic. The liquids seemed to diffuse with greater ease through the cuticula if some agent were present which kept it soft and pliable during the stages of dehydration, especially between 85 per cent alcohol and the clearing agent where the greatest difficulty was always encountered. In every case of shrinkage and collapse the indications were that diffusion pressures caused the damage and that, were a series of dehydrating and clearing fluids possible which had very similar diffusibilities or penetrabilities, the greatly unbalanced diffusion pressures arising during the passage of the material from one liquid to the next would be eliminated and with them the distortion of the specimens.

By the use of Carnoy-phenol, itself water free, the killing and dehydration processes can be accomplished at once in the following way: The material freshly collected and freed from adhering dirt and slime is placed in

CARNOY-PHENOL

Absolute alcohol	20 cc
Chloroform	15 cc
Glacial acetic acid	5 cc
Phenol crystals to raise the volume by	10 cc
Total	50 cc

If the fluid is too strong for very delicate worms, it may be weakened by the addition of a very small quantity of water. After killing the worms should be placed in the fluid of full strength before further operations are undertaken. With material so killed only two operations are required to bring the objects into paraffin or balsam, and one to clear them in glycerine; if killed in other media and stored in alcohol, three operations attain the same end. Nematodes may be taken from 70 to 80 per cent alcohol, glycerine, lacto-phenol, or formol in which they have been stored and placed directly in the fluid. Smaller worms are cleared almost instantly so that a rapid survey if desired may be made of their internal

organization after which they may be removed to 95 or 80 per cent alcohol for storage. If the larger specimens do not clear sufficiently at first, almost any degree of clearing may subsequently be obtained by allowing the fluid in which the worms are placed to evaporate, the degree of clearing being proportional to the amount of evaporation. Still greater transparency is obtained by adding glacial acetic acid and phenol to the worms.

With specimens now in the fluid they may be prepared either for sectioning or for mounting in balsam with equal ease. Oils of synthetic wintergreen and oleum cidri ligni (Merk) or chloroform may be dropped *slowly* into the dish with the specimens and mixed thoroughly by agitation. The progress of this clearing should be watched carefully under a binocular or compound microscope and if the slightest shrinkage is observed it indicates that the clearing is being rushed. The change of liquids must be very gradual especially at first when the tissues are hardening but as soon as the mixture is three quarters clearing fluid, the greater part may be drawn off and the pure liquid added more rapidly and allowed to remain for 10 to 15 minutes or longer. If now infiltration by paraffin is desired, the wax is shaved into the dish with the specimens in clearing fluid and the whole set aside in a slightly warm place for 2 hours when the worms may be placed in pure paraffin, melting at 58 C. and after proper infiltration imbedded and sectioned.

Following Carnoy-phenol fixation numerous stains work nicely on sections, preferably those stains which do not require taking the sections to water because in such cases the cuticula is likely to swell and tear loose the sections or parts of them. Delafield's or Ehrlich's hematoxylin in 50 or 70 per cent alcohol stain well followed by Orange G or some other counterstain. Among the iron-hematoxylins Dobell's works splendidly and is, for the reason mentioned previously, preferable to Heidenhain's, it is also more selective and does not require a watery mordant. Staining is accomplished in the following manner:

Sections are freed of paraffin and run down to 70 per cent alcohol in the usual way. At this point they are mordanted in 1 or 2 per cent solution of iron alum (ammonium ferric sulphate) in 70 per cent alcohol for one-half to one hour (or longer), rinsed in 70 per cent alcohol and placed in a 1 per cent solution of hematein in 70 per cent alcohol for a period as long as that of mordanting or longer. The sections after this treatment and rinsing in 70 per cent alcohol are ready for destaining which may be done rapidly in 0.5 per cent acid (HCl) in 70 per cent alcohol, but preferably, for more even results, in the mordant itself until satisfactory differentiation has taken place. The sections may be counterstained or not as one desires, cleared, and mounted in damar or in what is an excellent medium —cedar immersion oil.

Safranin O counterstained with lichtgrün produces a pleasing stain in which, however, the lichtgrün is dominant because of the few nuclei appearing in any one section of material. But the most pleasing stain of all for presenting differentiated pictures is obtained with Mallory's triple stain (Guyer 1917). By this combination of dyes all cuticular parts are colored in shades of blue to purple blue—with an occasional exception where it is orange red. Muscle tissue such as the contractile portions of the muscle cells of the body wall are brilliant red as also are the muscle fibres and bundles of the esophagus and other portions. Protoplasm is pink with a suggestion of a bluish tint; nuclei are darker red with brilliant orange nucleoli. Material fixed in Flemming's reagent and stained with Mallory shows less red with more yellow and purple shades; differentiation being even greater.

To mount whole preparations in balsam the procedure is the same as for sectioning, including the bringing of the worms into clearing fluid; wintergreen is here to be preferred to the other clearing fluids in general laboratory use because of its rapid penetrating power; xylol shrinks tissues too readily and should be entirely avoided. Now the Syracuse crystal bearing the worms in a small quantity of oil is tipped only slightly and a large drop of pure, unthinned, paper-filtered Canada balsam is placed on the sloping bottom of the dish away from the worms and the whole covered. The resin will flow slowly down and diffuse throughout the oil and specimens in the course of 2 or 3 hours. Should the resulting resinous mixture be too thin to dry rapidly upon mounting the objects, more balsam may be added as before. It is important not to rush this process because the thinner medium within the worms will move through to the exterior faster than the balsam can penetrate to the interior with the result that the pressure becomes less within than without and unless the cuticula is thick, collapsing will result; but in all cases the more volatile fluids will vaporize under this reduced pressure and fill the body cavity and interstices between the organs with gas so that the preparations are again valueless, being utterly opaque. If collapsing has not taken place, the difficulty may be remedied by thinning the balsam with chloroform or benzol until the bubbles are gone, then controlling evaporation until the thickness of the fluid is again suitable for mounting. However, should collapsing have occurred, and should the specimens be valuable enough to warrant saving, restoration may be accomplished by running the worms back to Carnoy-phenol and leaving them there until the collapsed portions have filled out. If this does not occur spontaneously, a slight manipulation by rolling the worm gently will usually restore shape but should this not be the case restoration by the lactic acid method may be used (Hetherington 1922).

Except for low power work with a microscope, toto staining is of little value in examination of relatively large specimens because of the marked

tendency it has to mask the finer details of structure which one is desirous of seeing when using higher magnifications. This is due to the deep and homogeneous coloration taken on by the cuticula and underlying structures belonging to the bodywall. Best results along the line of toto staining using Carnoy-phenol in the process were obtained by using Orange G, safranin, methyl green, lichtgrün, acid fuchsin, methyl blue, Mayer's HCl carmine and Ehrlich's hematoxylin.

With the exception of HCl carmine, safranin, and the hematoxylins, all these stains are used by adding the dry powder in very small amounts to Carnoy-phenol and the degree of staining controlled. Safranin is utilized to saturation in 70 per cent alcohol and allowed to strongly overstain the specimens. Then they are removed to Carnoy-phenol until destaining is sufficient when clearing is at once undertaken. Acid fuchsin is the most tenacious of the stains mentioned and colors very rapidly. The most presentable mounts were obtained by slightly overstaining the specimens in the phenol reagent with small quantities of acid fuchsin and lichtgrün added in powder form to make a dark purple solution. Then the cuticula and body-wall musculature are destained by placing the worms in 95 per cent alcohol and passing into it a small quantity of dry ammonium gas. When all color is totally gone and the specimens are white showing no clouds of red coming off, they are returned to pure reagent which again restores the red color, most of which is now only in the internal organs. Clearing and mounting are done as described previously.

Much greater latitude for observation is better obtained by utilizing degrees of clearing rather than staining. Permanent mounts may be made of glycerine-prepared specimens in glycerine jelly properly sealed against evaporation, or material may be mounted after suitable preparation either in camsal-balsam, cedar immersion oil, or Canada balsam. These four mounting media will give a differential clearing indicated by the following approximate indices of refraction: 1.476, 1.47, 1.520, and 1.535 respectively (Lee 1913). To prepare the specimens for passage into these media, they are first placed in Carnoy-phenol and then brought into the clearing fluids most suitable for passage into the mounting medium. For glycerine jelly mounts, the phenol reagent is replaced by pure glycerine; camsal-balsam is preceded by clearing the material in camsal, a liquid formed by the mutual solution of salol (phenyl-salicylate) and gum camphor; immersion oil follows thin cedar oil; and Canada balsam replaces oil of wintergreen. The process of clearing is accomplished as previously explained.

Another excellent medium for small, very transparent worms is "Diaphane," a resinous medium employing gum sandarac on the order of Gilson's "Euparal" which, because of its low index of refraction, shows greater detail in the cleared specimens than balsam. The nematodes are

cleared carefully from the phenol reagent by camsal and allowed to harden for a short time in this fluid. Then they may be transferred to diaphane, diluted to about one half strength by absolute iso-butyl alcohol, and allowed to clear by gentle evaporation of the alcohol. A slightly greater degree of clearing may be obtained by preparing the worms in the same manner and transferring to pure Canada balsam with 5 to 10 per cent camsal well diluted with iso-butyl alcohol. This, too, makes an admirable, but very slow drying, tough, elastic medium.

SYMMETRY AND STRUCTURE OF THE HEAD REGION

General Considerations

Type form of the primitive nematode

Ward (1917) has utilized for the purpose of grouping nematodes the structure of the anterior end, particularly the oral armature, and has contrasted three terms: lips, jaws, and capsule, each referring to a typical oral organization. As an example of true lips may be mentioned a member of the genus Ascaris (Fig. 42) as showing, when viewed en face, three lobe-like projections of which a large one, bearing two papillae, is dorsal, while the other two each bearing a single papilla, are ventral. The genus Camallamus (Fig. 33) illustrates true jaws. Here the armature is divided into dextral and sinistral halves which act as a vise for maintaining a hold on the host tissue. The capsule or third type may be found among the members of the group of Strongyles (Fig. 40). Here the vestibule is cup-shaped with a large roomy interior opening to the exterior by an oval or circular orifice. Within the vestibule and on the walls are various organs for cutting, piercing, gnawing, etc. A closer study of the cephalic region, its structure and symmetry may indicate the value of these suggested groupings or may indicate further groupings or means of relating the nematodes within any one category, or still further may serve to show which structure is the most evolved and of the highest type thus indicating the evolutionary status of the species or genus among the members of its genus or family respectively.

In order to obtain the proper perspective of the value of the cephalic structure either from a taxonomic or an evolutionary point of view, it is first necessary to consider what may be termed the primitive nematode, and then in this light determine whether cephalic organization has kept pace with or lagged behind the specialization of the nematode body as a whole, through which it is fitted to its environment. It is for this reason that the primitive nematode is considered in regard to its form and symmetry before the anterior portions of the free living and parasitic forms are discussed critically with reference to their symmetry and specialization in structure.

The great difficulty in such a definition or delineation arises in the determination of criteria for primitiveness. In general a primitive organism is believed to be one with the most generalized structure or in other words

an organism with the most avenues along which it may specialize. However, when one is confronted by a nematode which has organs or a system of organs that are structurally very generalized and at the same time other systems are very highly specialized, the question may be asked whether the simple structures have devolved or are hold-overs of the primitive type which existed in the ancestral nematode. There is naturally no adequate nor absolute solution to such a query and if any explanations are offered they can at best be based only on a critical examination of details in numerous free and parasitic species, each detail being selected with careful consideration of its stability in the stress of environmental factors.

According to Steiner (1919) the type form of nematode body is a spindle in which the principal axis is much elongated over the two similar dextro-sinistral and dorso-ventral axes. Any alterations in the relative proportions of these axes of the primitive form will necessarily alter profoundly the general outline of the body: with extreme lengthening, for example, of the principal axis and only a slight shortening of the other axes, or none, it is a very easy transition into such a filariform individual as an adult *Dracunculus medinensis* Velsch, measuring more than a meter and a half in length. On the other hand, lengthening of the two secondary axes in greater proportion than the principal axis would produce a form of adult such as *Heterodera schachtii* Schmidt, the common parasitic nematode of the sugar beet, the female of which at maturity becomes a swollen lemon-shaped individual.

In cross section the primitive nematode is always circular with no suggestions whatever of dorso-ventral or lateral flattening. Neither is there any evidence of metamerism, a fact which is borne out in extant forms in none of which there is the slightest suggestion of septa. In this connection it should be noted that there is also no coelom, the existing body cavity remaining as a derivative of the primary body cavity or blastocoele. Pseudo-segmentation is present in the cephalic bristles, according to Cobb, of about thirty per cent of the free living nematodes and in one form *Scaptrella cincta* Cobb, even the mandibles are jointed. However, this condition is limited only to the cephalic appendages and in no case, either in the embryo or adult, has any trace of true segmentation been observed in the body proper.

The mouth of the primitive form is terminal as in present forms, except a few genera in which it has become secondarily dorsal, notably in the genera of the family Ancylostomidae. Embryologically the mouth is subterminal ventrally and during development it migrates to the terminal position. There is, however, still a difference of opinion among investigators on this point; some believe that the blastopore as a slit-like opening closes completely from behind forward and that the mouth forms inde-

pendently in front by an ectodermal invagination; other workers believe that the definitive mouth arises from an incomplete closure of the blastopore giving here the ventral location of the mouth which shifts at an early stage to the terminal position. The anus, however, is ventral and posterior, which too is typical of present-day forms barring, for example, a few highly modified individuals such as the adult female of *Heterodera schactii* with a dorsal anus; *Trichosomoides crassicauda* Bellingham, members of the genera Trichuris Roederer, Eustrongylides Jägerskiöld, and Hystrichis Dujardin, in which the anus is terminal. In free living forms the anus is always posteriorly ventral and a tail is present through the tip of which three caudal glands pour out their secretions. These glands fabricate a cement-like substance which hardens in the presence of water and serves to hold the individual to the substrate of its habitat. The lack of a tail and the presence of a terminal anus as existing in the groups just mentioned do not seem to fit into the conception of the primitive nematode as will appear later in this discussion but they may be of significance in the conception of the ancestor of the primitive nematode, a discussion of which will follow in the course of this paper.

The openings of the reproductive systems of existing forms allow the products of the gonads to reach the exterior differently in the two sexes: by way of the rectum and anus in the male nematode and by way of the vulva in the female worm, an opening quite separate, generally on the ventral surface in the mid-line. It is believed by Steiner that the primitive nematode, male and female alike, possessed only one ventral orifice which was a common opening for the discharge of the reproductive elements and alimentary waste, as well as serving for the outlet of the excretory system. Such a primitive worm possessed a cloaca, which is present now in no known forms; indeed these three systems—alimentary, excretory, and reproductive—terminate in a great variety of positions in extant forms.

Contrary to the hypothetical condition, the excretory system with few exceptions opens mid-ventrally far anteriorly in the neighborhood of the nerve ring. The vulvar opening may be found posterior and terminal in the parasitic nematodes belonging to the genera Trichuris, Heterodera, Eustrongylides and Hystrichis, but more often it is near the middle of the worm in free living and parasitic forms alike. In Syphacia and some Oxyurids it lies far forward in the anterior half of the body—even close to the nerve ring. In the male organisms the gonads open by their ducts into the rectum in connection with the spicular apparatus. Beside these points in the foregoing paragraphs, the primitive nematode has a simple digestive tract, paired gonads, and paired excretory canals. These with all the other elements of the ancestral form are arranged in such a manner that the body is wholly bilaterally symmetrical.

Alterations in bilaterality of primitive type

Among the legion of nematodes existing now, strict bilaterality in which each half of the individual is a mirror image of the other, does not exist as far as known, at least in the adult forms. Some of the immature forms prior to their last moults more nearly approach bilaterality than do any of the adults for in them the gonads are present only in rudimentary form, lying in the mid ventral line. Changes in bilaterality are very easily brought about by any shifting of the relative proportions of the axes: any lengthening of the principal axis without proportionate concomitant increase of the other two axes would for mechanical reason alone produce a serial ordering of elements which had heretofore lain side by side in the body cavity. Evidence of this fact is to be found in the serially arranged testes of many of the free living nematodes and similarly the caudal glands have become serially ordered in a most striking manner (Fig. 22). The female reproductive system exhibits the largest number of variations in arrangement of its parts. The ovaries and uteri are double but the uterine ducts unite so that there is always one vagina and one vulvar opening. In general one ovary is reflected anteriorly and the other occupies the posterior portion of the body cavity, or in cases where the vulva lies far anteriorly or far posteriorly either the anterior or posterior ovary may suffer partial suppression or become entirely vestigial.

Such changes as these just mentioned alter the actual bilaterality but do not in any way change the fundamental bilaterality of the organism. Whatever the changes in symmetry which replace or become superimposed upon the bilaterality of the nematode as a whole, they are secondary features having arisen during the evolution of the primitive form into the present types of great complexity. Strict asymmetry is most noticeably present in the free living nematode, *Bunonema inequale* Cobb, and in related species which possess on the dextral side a row of immense tubercles giving the individual a curious unbalanced appearance. Such striking asymmetry is not very often seen and in place of it radial symmetry constructed on plans involving varying numbers of radii is much more general. In order to understand better, perhaps, the advent of this type of symmetry, it is necessary to consider the question of the orientation of the primitive nematode with respect to its surroundings. Steiner has discussed this question in considerable detail and his views in main will be outlined in the following few paragraphs.

Primitive orientation of nematodes

Whoever has dealt with free living or parasitic nematodes is aware of the fact that they always lie upon either the dextral or sinistral aspect of the body, so that their looping and twisting is in reality confined to the plane of their principal axis. The morphological ventral surface becomes a

lateral surface so that the actual creeping surface is in no way comparable for example to the creeping surface of the earthworm. The embryological evidence indicates that the actual adult and embryonic ventral surfaces are the same so that there can not have been any shifting of the anal, excretory, and reproductive openings to a lateral field. This fact proves that the mode of locomotion engaged in by most nematodes has been acquired as a secondary means of progression.

The primitive orientation was probably of such a nature that the principal axis was perpendicular to the substratum—the nematode being held in position by the secretions of the caudal cement glands. In this position the nematode could wave back and forth in a dorso-ventral plane simulating the waving movements of some of the tubificid worms. In support of this orientation are examples of some half sessile free-living nematodes (from fresh and salt water) which live on algae and aquatic vegetation and which may or may not possess eye spots. These sense organs are blackish or red pigment spots or pigment cups, each of the latter bearing over it a single transparent lens, as for example in the following worms:

Thoracostoma antarcticum von Linstow
Thoracostoma lobatum Steiner
Nemella ocellata Cobb
Ionema ocellatum Cobb
Onchulella ocellata Cobb (Figs. 21 and 30).

These ocelli with few exceptions are to be found far forward lying laterally upon the esophagus; only in a few cases do they lie slightly dorsal or ventral with respect to the esophagus. The lenses are so directed that light coming from a vertical source will fall upon them when the worm is oriented vertically. Should the primitive worm have moved normally on a side, as many of them do today, one or other of the eye spots would have been turned toward the substrate and would have thus become temporarily useless. Light to have stimulated both spots through the medium of the lenses with the worm so oriented would necessarily have come from a horizontal source which is improbable. Other nematodes, members of the genus Echilidium, possess pigment surrounding the esophagus and above this a circlet of ocelli set to collect vertically falling light.

Furthermore some free living nematodes possess many long delicate cephalic bristles, (*Monhystera pilosa* Cobb (Fig. 13), *Pomponema mirabile* Cobb) and others bear on their bodies many fine bristles (*Sphaerolaimus hirsutus* Bastian, *Notochaetosoma tenax* Irwin-Smith). These delicate processes can not be reconciled with a creeping mode of locomotion through sand, mud, and debris, but they are consistent with a half sessile form of existence. Still other species are parasitized by epizoa and epiphytes which cover all portions of the body. For instance, a delicate filiform alga often

covers the body of *Spira parasitifera* Bastian while vorticella may attach itself to the tail of the same worm. Such ectoparasites could neither remain attached to the nematode nor stand the wear and tear if the host thrashed about among debris and sand. According to Irwin-Smith, some members of the family Chaetosomatidae, which however are not clearly true nematodes, hitch along the rocks and vegetation in the manner of measuring worms by means of special adhesive bristles arranged in two rows on the ventral surface near the tail and by other adhesive bristles on the dorsal portion of the cephalic region. Seurat believes these bristles are a special adaptation. Some other free living nematodes according to Cobb's observations move as many rotifers do, in a looping fashion, using the caudal glands and suction created by the muscular esophagus as alternate means of fixation during progression.

The points reviewed in the foregoing paragraphs seem to indicate rather strikingly that the primitive nematode led a half sessile life, oriented in an upright or nearly upright position, as do many of the free living forms today. Another feature of interest in this connection, the sessile tendency, is the prevalence of radial symmetry in the anterior regions of great numbers of non-parasitic and parasitic forms. A characteristic of sessile animals like the Coelenterata is their radial symmetry, or like the Echinodermata their pseudo-radial symmetry, which has become superimposed secondarily upon their primary bilaterality. As a result of the sessile tendency among the free living nematodes, pseudo-radial symmetry would materially develop.

Definition of the primitive nematode

Steiner (1919) has defined the primitive nematode in short as a bilaterally symmetrical, spindle-shaped animal affixed to its support by the secretions of three adhesive glands at its caudal extremity, possessing a simple digestive tract with no diverticula or convolutions but with a muscular esophagus, having paired gonads in the two sexes lying parallel, one on each side of the intestine, throughout their length, their ducts opening with those of the paired excretory vessels and the intestine into a cloaca discharging by an anus to the exterior in the mid ventral line, slightly anterior to the termination of the tail. Seurat (1920) after a careful consideration of what he believes to be primitive characters still maintained in some of the present day nematodes, avoiding characters induced by adaptation to environment (parasitic adaptations like complex ovejectors, organs of fixation, buccal cavities armed with teeth, or free-living adaptations such as long cephalic bristles, ventral adhesive setae of the Chaetosomatidae, buccal stylets of Xiphinema and Dorylaimus, etc.), defines the primitive nematode as follows:

"Vermiform organisms of small size living in detritus or decaying

material in moist surroundings; bilaterally symmetrical; mouth subterminal, ventral, limited by three lips, one dorsal and two subventral; tails acutely conical, presenting three caudal glands which open at its point. Cuticula smooth, covered by scattered sensory papillae; epidermis of distinct cells; four bands, dorsal, ventral and laterals, separating four muscular fields; muscle cells of large size, few in number; lateral bands presenting scattered unicellular cutaneous glands.

"Buccal cavity tubuliform, short; anterior intestine (esophagus) elongated with tripartite lumen, lined interiorly by a cuticular membrane, differentiated into a clubshaped esophagus swollen at its terminal portion and a bulb with valves (proventricle); middle intestine of entodermal origin, formed of a small number of large cells, giving forth sometimes a dorsal cecum in its anterior region; terminal intestine short, lined by a cuticular membrane in connection at its origin with three unicellular rectal glands. Excretory apparatus paired, comprising on each side of the body an anterior canal and a posterior canal which come to open by a lateral pore where there also empties a unicellular gland. Sometimes this apparatus is double and admits of a second system of canals opening in the posterior half of the body. (This form is realized in some females of the genus Rhabditis opening alone without any single gland by a small pore laterally situated in a band of muscles.)

"Sexes separated; sexual dimorphism faint, the male being characterized simply by a richer development of papillae in the presence of the sexual orifice. Genital glands paired; the two genital tubes of the male being differentiated into testicle, vas deferens and ejaculatory canal opening a short distance in front of the anus and extending in parallel toward the anterior portion of the body; two cement glands empty into the proximal region of the ejaculatory canal; copulatory organs represented by two equal spicules sliding in an unpaired groove (gubernaculum). The female apparatus is formed of two tubes differentiated into ovary, oviduct, uterus and vagina, opening anterior to the middle of the body and extending in parallel course toward the front; ovaries clublike, oocytes not very numerous; uterus serving for storage of a very small number of large sized eggs, borne only to a slight stage of development. The number of genital tubes may advance sometimes to two or even three pairs.

"Eggs homo-lecithal, with clear cytoplasm; segmentation total, unequal. The larva leads a free existence comparable to that of the adult and undergoes four moults in the course of its evolution or growth, its principal increase in size occurring at the moments of these moults, (a character conserved in *Cephalobus ciliatus*). The genital organ is represented in the hatching larva as an unpaired group of two germinative cells and of two somatic cells; this group which remains unpaired throughout

life develops only very slowly in the course of the second half of the larval life."

There are no known living forms which possess all the primitive characters set forth either by Steiner or Seurat. The latter author makes no statements regarding primitive spatial orientation and further regards the three-lipped form—with one dorsal and two ventral lips—as the probable early type while the former author postulates a simple digestive tract devoid of diverticula. Among the free living nematodes members of the genus Rhabditis have conserved some of the primitive characters in the structure of the digestive tube and genital organs but have gone far afield in the acquisition of a radial symmetry of the mouth, in the reduction of the male genital system to a simple tube and also in the structure of the lateral lines. On the other hand, among all the parasitic nematodes, those guarding the most numerous primitive features are the members of the oxyurid group. They possess primitive musculature, and show primitive structure of the lateral bands, the excretory apparatus and the digestive tube. Contrary to these ancestral features are the extreme modifications of the ovejector in the female and of the spicular organs and truncated tail of the male. The larvae are, however, rather undifferentiated and afford some of the data upon which the primitive nature of the group is based.

Cephalic Structure in Free-living Nematodes

Symmetrical type of the esophagus

After the preceding discussion of the primitive nematode, its bilateral nature and orientation, the following sections will be limited to a consideration of the structure and symmetrical content of the cephalic region (1) of free-living species, and (2) of parasitic species, in an effort to determine the primitive condition and the successive changes which evolution has imposed upon the early type.

One element of the anterior region which is ever a possessor of triradial symmetry in all the members of the Myosyringata Ward (1917) is the esophagus. In cross section, this organ exhibits a triquetrous lumen, "sechseckig" as Schneider (1866) calls it, with three alternating obtuse angles directed apex lumen-ward, the other three, acute angles, apex outward. Of the three portions into which the muscular tube is divided, one-third is always dorsal and the remaining two-thirds are subventral, so that one of the obtuse angles mentioned is always directed ventrally. The few exceptions existing to this type of esophagus have been placed in the group Trichosyringata Ward, a group characterized by the possession of a capillary esophagus. The morphology of such an esophagus has not been carefully worked out so that as yet statements regarding its symmetry and structure are not on a substantial basis. It may be that some of the

genera in that category will have to be removed from it as not being related, such as *Trichosomoides crassicauda* Bell, which, according to Rauther, shows a triquetrous esophagus, at least for a considerable part of the length of that organ.

The triradial nature of the esophagus is such a distinctive feature of the phylum Nematoda and is so nearly universal throughout the group, that it may be accepted as one of the most stable factors in nematode organization. For this reason, it may be considered a primitive feature; certainly, if not primitive, it is one of the earliest features to have been established in the evolving ancestor. When this triquetrous organ, which underlies all the superficial structures of the cephalic region, is used as the basis of determining the symmetry of the head, the only possible symmetrical divisions involving all structures would be two in number; namely, one of bilaterality, and one of triradiality, the latter of which by division of sectors might readily pass into conditions of multiple symmetry among the more superficial structures like the lips. Exceptions to triradiality would, of course, occur in nematodes possessing cephalic branches to the lateral excretory canals, amphids and ocelli. Normally radiality merges progressively into bilaterality as the region of the nerve ring is approached in an antero-posterior direction, suggesting rings or horizontal planes of symmetry appearing at different levels of the cephalic region. The more anterior structures are more truly arranged radially symmetrically while those later succeeding levels as has been said pass into bilateral groupings.

When, however, the more superficial structures of the nematode head and pharyngeal region are examined, these fundamental di- and tri-radial symmetries give place to curious mixtures of symmetrical patterns in one and the same nematode, involving plans based on multiples of two and three radii. Lips, papillae, sensory hairs, cephalic bristles, teeth, and cuticular processes are compounded in a variety of ways; for example, *Oxyuris obvelata* Rudolphi bears three lips arranged in correspondence with the three sectors of the esophagus but the six papillae are grouped in a dextral and sinistral row of three each (Fig. 1). *Protospirura muris* Gmelin carries a right and left row each of three lip-like divisions and four papillae, one at the base of each terminal division of each row (Fig. 10); again, the elaborately constructed *Mononchus gerlachei* de Man, a marine nematode, possesses six radially arranged lips each bearing, centrally placed, a single papilla and at a lower level each carrying two papillae save the two central lateral lips which have again only a single papilla each. Immediately below the lips on the walls of the vestibule are twelve rounded projections of unknown significance. Beneath these there is a chitinous skeletal structure hexagonal in optical section merging into the triangular lumen of the pharynx which itself passes into the ever present triquetrous esophagus (Fig. 3).

These examples were chosen at random from countless other similar, simple and still other beautifully intricate forms merely to show the variations possible, of which the last specimen (*Monochus gerlachei*) illustrates symmetry built on two, three, four, six, and twelve radii. Yet this last whole complex arrangement really becomes bilateral because of the unpaired median lateral papillae and a very large dorsal tooth not previously mentioned, situated on the roof of the buccal cavity about midway between the oral aperture and the esophageal region in the mid-dorsal plane.

Pharyngeal modifications

Turning now to a closer study of cephalic structure, one finds among some of the marine nematodes head regions remarkably simple from the standpoint of structure whereas from the point of view of their genesis they may not perhaps be termed simple in the sense of meaning primitive; however, this point will be reconsidered in another section. In genera belonging to the order Litinia Cobb 1920, there are forms in which the head is devoid of lips; papillae are indistinct or minute; no pharynx is present; the esophagus is simple with no bulb; and cephalic bristles may be absent. *Litotes minuta* Cobb is extremely simple for the mouth opens directly into the esophagus; no lips or bristles are present, but papillae —six in number—exist; the body as a whole is rather simple and the amphids are very indistinct. In *Alaimella cincta* Cobb, the head possesses a simple mouth surrounded by six papillae and probably six flat amalgamated lips which can scarcely be comparable to lips as defined by an example of Ascaris in a previous portion of this paper. There are also four cephalic bristles present in this species. A related species, *A. truncata*, the type for the genus Ailaimella, has similarly four bristles and six papillae and in the male two testes are present, indicative of a primitive nature. *Ionema ocellatum* Cobb possesses two ocelli with lenses directed anteriad, a simple circular mouth, no pharynx, no lips, and four cephalic setae. *Schistodera exilis* Cobb and *Tycnodora pachydermata* Cobb similarly have circular mouths; however, the former bears four minute papillae around the mouth and the latter, two circlets of setae, the first and anteriormost composed of six and the second, of four. Each one of the nematodes just mentioned lives free upon algae and "seagrass" or upon the sand at the bases of this vegetation.

Still other marine forms possessing no pharynx and a simple mouth circular in outline, devoid of any form of lips, are members of the interesting family Chaetosomatidae. These nematodes are not strikingly organized in structure except in the remarkable possession of ventral adhesive bristles on the posterior portion of the body and dorsal cephalic adhesive bristles or setae, which according to observations by Irwin-Smith are utilized in creeping. In this direction these forms have specialized to a

degree. Also the genera Ionema, Schistodera, and Nemanema of Cobb, and Thoracostoma Marion have this simple mouth and lack a pharynx.

Next in simplicity are nematodes which not only have a simple circular mouth with none or amalgamated lips, (*Terschellingia longicaudata*, *Monhystera stenosoma*) but also possess a pharynx. The pharynx is one structure which is subject to the greatest diversification and is to a great extent indicative of height of specialization and adaptation in free living forms and also among parasitic species.

Nemanema simplex Cobb, a marine algae-inhabiting nematode, exhibits a very simple cephalic region; bristles are absent; the mouth is a round orifice, surrounded by possibly six exceptionally indefinite papillae, and the pharynx is the merest conoid suggestion. This pharynx, almost unnoticeable in the form above, may become greatly elongated (*Rhynchonema cinctum* Cobb) and constant in width; short and narrow (*Litonema nudum* Cobb); or cavernous and greatly modified as in the genus Mononchus Bastian (Fig. 12) notably, and also in many others. The very undifferentiated conoid pharynx and its derivatives attained chiefly by elongation are prominent in nematodes living on a more or less liquid diet. In general, too, the enlarged and widened pharynges are greatly modified by armatures of onchi derived from their walls. Such are to be found among nematodes living upon a solid diet demanding more or less maceration. A very special type of such a pharynx is found among the spear-bearing nematodes obtaining food by piercing and then sucking the fluids, for example, from the roots and tender shoots of either water or land inhabiting plants.

There are, of course, intergradations among the pharynges such that one may arrange a series beginning with nematodes possessing no pharynx (Litotes) followed by forms with larger but unarmed pharynx which in turn pass into other forms bearing teeth among which the simpler ones bear three teeth, one each in a position corresponding to the respective sectors of the esophagus (*Mesonchium poriferum* Cobb). The tooth-bearing type, perhaps by further modification, passes into the spear-bearing nematodes such as Dorylaimus, Heterodera, Dorylium, Eutylenchus, Tylenchorhynchus, etc. Among the Mononchs the dorsal tooth is very large and works in opposition to the teeth belonging to the subventral sectors of the pharynx. The teeth on these last two portions may be very small and there may be only one per section as in *Mononchus radiatus;* they may be small and accompanied by numerous denticles (*M. dentatus* Cobb), or by two rasp-like structures approximated near the mid ventral line of the pharynx so that they may operate against the large dorsal tooth (*M. muscorum* Bastian); or further there may be no ventral onchi at all (*M. zschokkei* Mengel). The pharynx is partially mobile in some forms by means of three seams or hinges, one ventral and two lateral and a bit dorsal. In other cases where the walls of the cavity appear immobile, the lips seem

to force the food down upon the teeth and rasps by which means it is torn apart and made ready for swallowing.

Another type of armature is that found in *Synonchium obtusum* Cobb. Here what is apparently the pharynx is highly muscular and forms a large muscular bulb. The mouth is really the large flaring, triangular opening to the pharynx located in a slightly shallow depression formed by the six double, amalgamated, flaring lips. The sectors of the pharynx are equal and each is armed in its mid line by a mandible mounted by three in-pointing teeth and flanked on each side by a small tooth (Fig. 16). When the pharyngeal bulb contracts, the mandibles are approximated, drawn inward and downward while the lips are slightly raised, partly covering the mandibles. Another nematode, *Xyala stricta* Cobb, has three similar but less elaborate mandibles. Still another example of the open flaring and armed pharynx may be found in *Gammanema ferox* Cobb. Here the base of the pharynx is armed with three ribs, each bearing an inward pointing onchium. Jointed mandibles (Fig. 7) are present in *Scaptrella cincta* Cobb, and inpointed ones are again present in *Cheironchus vorax* Cobb and in Selachinema.

There are forms which have greatly developed dorsal onchi which have become in many cases much elongated (Anaxonchia) and well buried in the esophageal musculature. These spear-shaped onchi are movable and perhaps they form, as Cobb has suggested, the transition from the pharynx armed with onchi to the spear-bearing pharynx. There is still another spear-bearing group in which the so-called stylet is hollow, allowing the fluids to be drawn through it by suction created in the esophagus. Dorylaimus and Discolaimus are good examples of this construction. Some species indicate by the structure of their stylets that these organs may have arisen by the partial fusion of three onchi and a few of them distinctly show construction from three portions (*Tylopharynx striata* de Man). It may be possible then that by certain developments during the evolution of these trionchiate forms, a partial fusion of the onchi has taken place with an accompanying elongation and narrowing of the pharyngeal cavity giving rise eventually to the hollow pharyngeal stylet. Each of these pharynges has its symmetrical content, but these relations will be considered in a following section in connection with oral structures.

Oral structures among nematodes

The oral structures of the free living nematodes are equally as complicated as the pharyngeal and show almost as numerous variations. The simple circular mouth, noted in connection with some of the nematodes mentioned in a preceding paragraph as possessing no pharynx is, one may say, the simplest from a structural standpoint, but whether it is the most primitive form cannot yet be said. In view of the fact that the esophagus

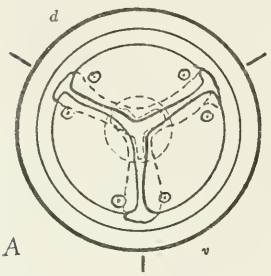
is triquetrous, it would appear that the most primitive form of mouth would not be a circular orifice but rather a triquetrous or triangular opening agreeing in symmetry with the esophagus; however, either view might be taken and some considerations which will follow later will support the former view that the primitive mouth opening was round. In *Thoracostoma setosum* v. Linstow a triangular mouth occurs but in consideration of certain specializations in the head region, it might better be interpreted as a fusion of three lips.

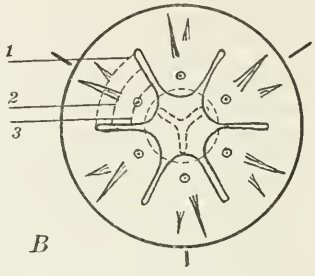
The next structurally simplest form and the one at present conceded most primitive is that found among members of the genera Enoplus and Rhabditis. The most primitive type of free living nematode in the estimation of nematologists is found in this last genus, where the mouth is surrounded by three lips, which are in fact definite and well formed. One of these is dorsal and the other two are subventral corresponding again with the divisions of the esophagus. The lips may be entire or there may be signs of division as in *Rhabditis pellio* Bütschli where each lip is divided incompletely into two portions by a shallow groove running longitudinally along its mid-region. Similarly *Rhabditis lambdiensis* Maupas possesses three lips distinctly bilobed, each bearing a pair of prominent setiform papillae, all equal and exhibiting as a whole perfect radial symmetry of the head region.

Quite in contrast to the division of lips may be mentioned the curious labial variations found arising from outgrowths of the lips in the genera Teratocephalus and Cephalobus. In the species *Teratocephalus crassidens* de Man the six lips surrounding the shallow pharynx have cuticular wings on the edges, partially fused near the bases of these lips, such that there results a corolla-like structure with a continuous edge. The apices of the four sublateral lips bear each a fine bristle (Figs. 2 and 4). On the other hand *Cephalobus ciliatus* von Linstow has arising from each of its three lips a thick column which bifurcates and gives forth two rather long processes whose edges are beset with bristles at regular intervals (Fig 6). In a position alternating with the lips, the cuticula near the periphery has become elongated into a stout horn-like process. The significance of such diverse outgrowths of lips as represented in the two genera above is not yet known. The radial symmetry of the heads in these two species is only superficial because just below the lip region on the lateral fields lie the amphids, one dextral, and one sinistral. They perforce shift the symmetry to bilaterality.

Evidence gathered from an examination of numerous free living nematodes seems conclusively to show that forms having a small number of lips acquired these labial organs by the subsequent division of the primitive three lips. Six lips are a very common number among many genera and appear as suggested by Rhabditis to have arisen by the division of each

of the three lips of the primitive form into two parts (Text figs. A and B). Division, tho incomplete, of these six lips gives rise to twelve lipped forms such as *Anaxonchium litorium* Cobb; complete division, to twelve small lips as *Iotodorus punctulatus* Cobb, and perhaps to the twelve highly modified lips or labial setae in *Pomponema mirabile* Cobb. Division of lips would then indicate a more evolved nature than the three lipped condition. This fact seems to be well borne out because many lipped forms occur among genera which have rather elaborate pharynges (Mononchus), and which have specialized in other lines too, like choice of habitat, loss of structures, as caudal glands and of one gonad by suppression. The Mononchs are to a large extent land inhabiting predatory nematodes rather more advanced in this last respect than their fresh and salt water relatives. The six lipped condition permits the oral aperture to open widely allowing the mononch greater certainty in seizing its prey and macerating it against the pharyngeal onchi.





Text Fig. A. Diagram of nematode head en face showing a simple radial symmetry with three lips. *d*, dorsal; v, ventral.

Text Fig. B. Diagram showing six lips derived by division of the primitive three. The superficial symmetry is multiradial; the deeper symmetry tri-radial on account of the esophagus. 1, 2 and 3 indicate rings of symmetry previously mentioned in the text: anteriormost, the ring of papillae; next, posteriorly, a ring of long cephalic bristles; and third, a ring of lesser bristles.

While specialization may go in one direction, namely, division of lips, still further specialization even in advance of division results by the union or amalgamation of lips. Degrees of confluence or amalgamation may be easily seen after a survey of a large number of species. For instance, one may begin with a form possessing three distinct lips (Rhabditis) and these may then become confluent as in *Monhystrium transitans* Cobb. The mouth opening resulting in such a case is triangular or triquetrous. *Monhystera stenosoma* de Man seems to indicate this even better than the preceding species. By far the most common number of lips is six, and

they offer many interesting variations, finally becoming confluent and forming a mouth capsule generally in connection with a large cavernous pharynx or buccal cavity. Among the Mononchs as previously mentioned, there are six lips which in many species are very well defined and separated (*Mononchus regius* Cobb) and in others the six lips exhibit various stages of union, for example, in *Mononchus major* Cobb the lips have become more rounded and less distinct so that the mouth opening assumes a hexagonal outline; in another genus and species, *Bolbella tenuidens* Cobb, the mouth has become a perfect circle and the six lips have lost entirely their individuality externally, but internally the organization still indicates the individual lips. An interesting feature, too, of this species is its asymmetry; the amphids, instead of being mid-lateral, have shifted slightly and occupy a dorso-lateral position and contrary to the general rule the dorsal onchus is not the one which has become specialized but instead the sub-medial dextral onchus has elongated and assumed a spear-like nature.

A characteristic feature of the genus Anguillula is the entire lack of lips; however, the papillae and internal arrangement of cuticular structures indicate very distinctly that the capsule is the result of completely fused lips, six in number (Fig. 5). In longitudinal section the mouth cavity is definitely divided into two parts; first an upper vestibule, thin walled, with the concave surface facing inward. This portion has probably arisen from the under surface of the fused lips. These organs in many lipped forms have a tendency to become thinner and less distinct so that one might easily expect them to become still less thickened after fusing and losing their identity to a greater or lesser extent. Following this vestibule (in *Anguillula aceti* Müller) there arises the pharynx properly speaking, set off from the preceding structure by a distinct break in the cuticular wall of the buccal cavity (Fig. 14). The lining of the pharynx is much thicker and, as seen in cross sections of the pharyngeal region, the lumen of the canal is triangular. The walls of the canal exhibit cuticular thickenings, one in the mid-line of each sub-ventral sector, which are opposed to a small triangular tooth in the mid-line of the dorsal sector.

A similar distinction between pharynx and vestibule may be seen in *Monhystera stenosoma*. Here the capsule has arisen from the fusion of three lips. Cephalic papillae are not definitely known to exist but the head bears in addition to the two lateral amphids four pairs of submedian bristles, the anterior-most member of each pair appearing slightly shorter than the other.

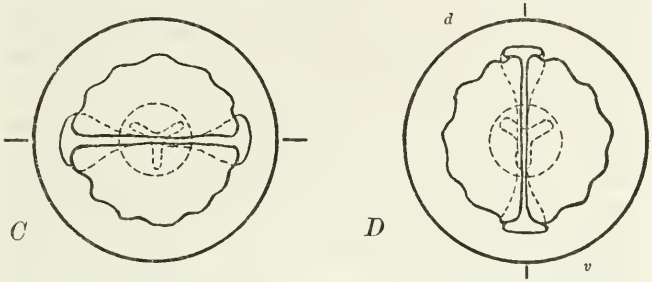
Turning now to a consideration of the oral organization among the spear-bearing nematodes, one finds lips again having undergone fusion either partial or complete. Complete fusion occurs in the genus Tylencholaimus, but evidence possibly of labial structure still remains in the presence of six papillae surrounding the mouth. Other genera, Tylenchus

and Dorylaimus, exhibit the same general structure but some of the species among the numerous ones in the latter genus show distinctly the lip-like nature. The fusion is complete enough to produce a circular mouth opening but the peripheral outline of the crown of lips viewed en face is scalloped showing the external outline of six lips (*Dorylaimus labiatus* de Man). There seems to be in these spear-bearing forms, derived from others possessing armed pharynges, an interesting correlation between extent of lip confluence and pharyngeal specialization. The mononchs with wider but less complex pharynges, from the standpoint of genesis, possess less confluent lips. In this connection one may ask whether the forms cited in an earlier portion of this section as possessing no trace of lips or pharynges have never acquired a pharynx or lips, or whether these structures have been lost by devolution, or whether they may indicate a greater stage of evolution. It cannot be said definitely at present which view is the better one to accept but in consideration of the primitive nature of the gonads in some of those forms it is quite possible that the weight of evidence favors the view of primitiveness.

Another interesting oral and cephalic structure and one which might be interpreted as the forerunner of jaws is to be found in *Synonchium obtusum* Cobb, which was described in connection with pharyngeal modifications. The six double lips have fused completely showing only a continuous crenate rim, as it were, surrounding the large flaring triquetrous mouth and pharynx (Fig. 16). Incidentally this nematode possesses pure tri-radial symmetry as far as the level of the amphids which shift the total symmetry of the head to bilaterality. By the transition from lips to jaws bilaterality becomes the only symmetry in the head region. The apparent change from the bi-radial pharynx to jaws comes through the loss of the dorsal sector of the pharynx accompanied by a lateral shifting of the other two sections. *Selachinema ferox* Cobb illustrates this change very beautifully because there remains a vestigial dorsal sector which, however, is greatly overshadowed by the two powerful submedian chitinous jaws. Another species yet undescribed by Cobb shows no remnant of this dorsal sector. *Chieronchus vorax* Cobb by a similar elimination of the dorsal sector has two jaws or mandibles. *Pseudonchus rotundicephalus* Cobb again supports the formation at least of bilateral mouth parts from the loss of the dorsal pharyngeal sector. So far there is no evidence which supports the view that submedian sectors ever fuse giving rise to jaws which work in apposition dorso-ventrally.

Perfect disymmetry in a dextro-sinistral sense (Text fig. C) is found in the three extraordinary genera, Diploscapter, Wilsonema and Heth, of which *D. coronatus* (Maupas), *W. capitatum*, Cobb, and *H. juli* Cobb are respective examples. The first possesses four strong outwardly directed hooks, two dorsal and two ventral and between them laterally are two

serrated flaps or lips, one right and one left. Cobb interprets in his illustration of this species the two flaps as well as the four hooks, each as a lip. If this is true, the nematode possesses six lips; the two laterals having flattened out and become flaplike; the two dorsals and two ventrals having fused and formed a single dorsal and a ventral double hooked structure. The second species above is distinguished by dorsal and ventral double "combs" and two lateral columns, a dextral and a sinistral one, tipped each by a finer process. Here the disymmetry is most prominent dorso-ventrally (Text fig. D). The last species of the three evinces again lateral disymmetry.



Text Fig. C. Diagram of nematode head en face showing disymmetry with respect to a dextro-sinistral plane.

Text Fig. D. Diagram showing disymmetry with respect to a dorso-ventral plane. Both this type and the foregoing are forms of bilateral symmetry.

Considerations of symmetry in the head region

After the considerations of esophageal, pharyngeal, and oral structure in the preceding paragraphs, the following ones will be devoted to an examination of the symmetry of the nematode head as a whole, considering the parts played by these structures in determining this symmetry. In view of the fact that the outstanding symmetry of the nematode body as a whole is bilateral, the same relation must have applied to the cephalic region in the primitive form, a fact which seems to be borne out by what is known of nematode embryology, and by features which nematologists have come to accept as primitive. The primitive mouth was ventral and the esophagus arose from three rows of cells, the dorsal one of which was the equivalent of the other two. These features alone would establish bilaterality in the embryo and in the primitive adult.

By an equalization of the three esophageal sectors, the triquetrous and the trisymmetrical nature of this organ became apparent. The primitive nematode had three lips corresponding to the symmetry of the esophageal sectors giving rise ultimately to a purely trisymmetrical structure. Only very few radially symmetrical cephalic regions exist among nematodes

today, because there are in the free living species organs such as amphids and ocelli, and because there are with or without these parts, the cephalic bristles and sensory papillae which in a great number of forms fall into a bilateral arrangement, despite radial ordering of other structural elements. In an otherwise radially symmetrical head, one often finds only four cephalic bristles instead of six, as if the median lateral ones had been lost and in cases of duplication of bristles or papillae on the lips, the lateral median lips are the ones which lag behind the others in this respect.

This peculiarity is well illustrated by Cobb as existing among the mononchs in relation to the labial and cephalic papillae. The arrangement of papillae in these forms follows the law for the arrangement of tactile cephalic setae of nemas in general, namely: " . . . When six are present one is found on each of the two lateral lines and one on each of the four submedian lines; when more than six are present, the increase occurs first on the submedian lines, the commonest number being ten,—one on each lateral line and two on each of the four submedian lines; when the number is in excess of ten, the increase is again more commonly found on the submedian lines." Obviously structures following this order of arrangement shift apparent radial symmetry into bilaterality again. Radial symmetry with few exceptions is actually attainable only if lips alone are concerned, as has already been shown.

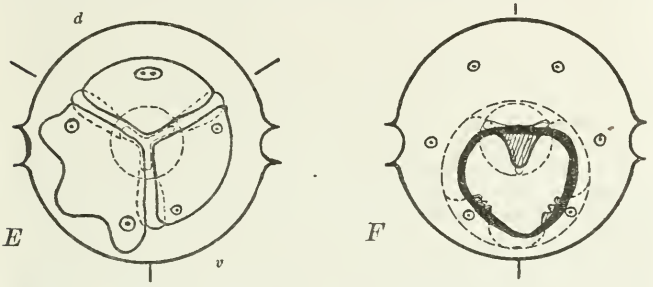
The pharyngeal region is frequently non-radially symmetrical, rarely is this not true, when it becomes armed with onchi (Text fig. F) because the dorsal ones usually have a tendency to surpass in size the other onchi. The small, smooth, prismatic or cylindrical, and unspecialized pharynx readily falls in lines with any symmetry which the lips impose upon it. Disymmetry either dorso-ventral or dextro-sinistral exists, as we have seen (Text figs. C and D), in a few free living forms. Its origin is explicable in a few cases as the result of loss of the dorsal lip and pharyngeal sectors. In such cases the cephalic symmetry shifts undeniably into the fundamental bilaterality. Asymmetry occurs least of the other types. In summary it appears then that true radial symmetry is not as general a condition among nematodes as a superficial examination would lead one to expect. Radial symmetry, however, is common, and a striking feature if sensory organs, pharyngeal onchi, and other armatures are neglected or considered secondary in importance to the basic plan of the head region. The apparent order of symmetrical succession in the nematode body beginning with the primitive worm is most probably the following, applied, of course, only to the cephalic region:

1. Primitive bilaterality
2. Radial symmetry (Text figs. A and B)
3. Disymmetry (Text figs. C and D)
4. Asymmetry (Text fig. E)

Cephalic Structure in Parasitic Nematodes

Symmetrical type of the esophagus

What has previously been said regarding the symmetrical factor of the esophagus in free-living nematodes is true of the parasitic forms also, at least those possessing the characteristic triquetrous muscular esophagus. Those nematodes having a capillary esophagus referred to as belonging to the group Trichosyringata comprise a restricted number of genera, among them being Trichinella, Trichuris, Trichosomoides, Capillaria, etc. Species belonging to these genera have no free-living larval forms and depend for distribution not upon any migratory effort on their own part but rather upon direct transmission of the embryos or eggs into the new host. Trichina, as is well known, is spread by the ingestion of the uncooked



Text Fig. E. Diagram of a nematode head en face showing asymmetry.
Text Fig. F. Diagram showing a typical case of bilaterality in a capsulated cephalic region.

flesh of the host containing the encysted immature worms. The gravid female of *Hepaticola hepatica* Hall dies in the liver tissue of the host, leaving there a mass of eggs which have no way of reaching the exterior or attaining a new host. In such a case, cannibalism seems to be the only agent upon which the species can depend for propagation. From the point of view of such extreme parasitism in this respect and further from the loss of one or both spicules of the male, the absence of one testis and one ovary in the respective sexes and the oviparous or ovoviviparous condition of the female, one might be justified in suspecting that the capillary esophagus is a degenerating one, departing in this respect from the normal form. With regard to the symmetry, this type is bilateral, if the row of large nucleated cells of the structure is dorsal and the capillary tube remains in a ventral median position, or if the tube being intra-cellular, lies within the dorso-ventral plane.

Cephalic modifications and relations to habitat

The transition from a free to a parasitic mode of life brings with it profound modifications in the organism. These changes are most admir-

ably seen when a comparison is made of the fascinating and intricate structure of the head region of free living nematodes with the gross and generally monotonous anatomy of that portion of the parasitic species. Sensory bristles, cephalic setae, ocelli, and other sensory structures as well as the amphids found in free forms are among the first organs to disappear after the assumption of parasitism. Then the digestive system is progressively altered most noticeably in the cephalic region, viz. the oral and pharyngeal structures. Concomitant with the general simplification and loss of structures, there is a rather progressive hypertrophy and complication of the reproductive systems, because as parasitism increases the chances for propagation are less favorable. Further adaptations are seen in the production of cuticular cephalic expansions, as the lateral alae of *Oxyuris tetraptera* von Linstow, the cuticular bosses of *Gongylonema musculi* Neuman, the ventral cuticular combs or spines of Rictularia, or the hook beset head of Echinocephalus, etc., which are only a few of the possible variations. In a general way, these outgrowths are adaptations which form excellent hold fast organs, as they are found only among those species which inhabit the alimentary canal.

At this point it might be well to consider the possibilities of specialization of the nematode parasite with respect to its habitat. Specialization among the parasitic species is usually the opposite of that among free living forms, for with few exceptions (hold fast organs and reproductive organs) the term implies a simplification or a loss of existing structures. The roundworms living in the posterior and anterior portions of the alimentary system of their host more nearly approach the free living forms than any others. For example, those living in the ceca and large intestine (Oxyuris, Ascaris) live largely upon the bacterial flora because most of the split proteins and carbohydrates of the digested food have been removed from the intestinal contents by absorption long before these regions are reached. In the stomach little actual hydrolysis of the food is accomplished so that nematodes inhabiting this organ must use and digest to a large extent the food presented them by the host. This fact is demonstrable in *Protospirura muris* inhabiting the stomach of the common mouse, for in this species, the intestine is usually filled by minute fragments and starch granules derived from the host's diet of grains. Other species such as those of Ancylostoma actually feed upon the cells of the intestinal papillae according to the observations of Looss.

From a parasitic point of view, the most highly specialized nematodes are those inhabiting the circulatory system (Filaria), the body cavity and the connective tissues (Gongylonema and Dracunculus). They must needs depend for their nourishment upon the absorbed food products circulating in the blood and lymph with which they are bathed and from which they osmotically acquire the necessary elements for their own metabolism. One would expect in such a case to find a correlation between

extent of parasitism in connection with cephalic structure, and such is indeed true as will come out in following discussions.

Pharyngeal modifications

Pharynges among the parasitic round worms are not as diverse in form nor as complicated in structure as many of those in the free living nematodes. There are no intergradations from a simple conoid pharynx, through the various changes of size and armature to the fusion of parts and formation of spears which one finds among the nonparasitic genera. Indeed the pharynges are few and are prominent only among the Strongyles where one finds them exceptionally well developed. The spear-bearing forms exist only among the phytoparasitic nematodes as Heterodera and Tylenchus but, as these round worms are to a large extent free living, they cannot be adequately classed with the more fully parasitic animal forms.

The simplest pharynx is really little less than a circular vestibule in many species; for example, *Protospirura muris* (Fig. 10) illustrates this quite well as a short cylindrical or faintly prismatic passage leading from the lips into the esophagus. Other instances of such a simple pharynx may be found in such nematodes as *Eustrongylides ignotus* Jägerskiöld and related species. The most elaborate pharynges are, however, found among the Strongyles where they are often large and capacious, almost smooth, or else armed by teeth and cutting plates. These structures are prominent among the characteristic features of the tribes Strongyleae, Bunostomeae, Ransomeae, Cylicostomeae, and a few genera of undetermined tribal relations. But since this capsular formation is so intimately connected with oral structure, its nature will be described in the following paragraphs in connection with modifications of the lip region.

Oral structure and symmetry

When the oral armatures of the parasitic nematodes of the alimentary tract are examined, one finds as a common thing various modifications of lips unarmed or armed with teeth or cuticular thickenings. Three lips are present in the most primitive of parasites, namely genera of the Oxyuridae, Heterakidae and Ascaridae, of which the members of the last family show a great number of modifications. In *Heterakis papillosa* Bloch the three lips are small and equal. A similar equality and tri-radiality exist in *Falcaustra siamensis* Baylis; the lips are somewhat flattened antero-posteriorly except for two prominent papilla bearing projections on each (Fig. 17). *Crossophorus collaris* Hemprich and Ehrenberg, probably an Oxyurid, is tri-symmetrical in every respect save the minor difference between the arrangement of the labial papillae which are two to each lip, but the dorsal lip bears them both at the same level near the lateral borders while the subventral lips carry one papilla a little to the ventral side of the middle of the outer lip surfaces; the other papilla being much smaller

and more anterior with respect to the first (Figs. 15, 37, 28). This might indicate a stage in the disappearance of two papilla, giving way to the more general condition of four cephalic papillae in the ascarids and furthermore this would also make the bilaterality of the ascarid head more pronounced.

Often between the lips of the ascarid type the cuticula and parts of the tissue lying beneath it are raised up into what has been termed interlabia. They fit nicely between the lips and where they are well developed they have been misconstrued as extra lips. The size and form vary from only small projections to a size subequal to the lips themselves as in *Ascaris nasuta* Schneider and *Ophidascaris mombasica* Baylis. Other labial variations arise by branchings of the pulp in each lip into diverse forms (*Polydelphis quadricornis* Wedl) or by partial division into multiple lips from grooves extending longitudinally over the lip (*A. holoptera* Rud. and *A. osculata* Rud.).

An interesting change occurs in the apparent tri-symmetry of the three lipped cephalic structure when diminution of the dorsal sector in some forms and final loss of it in others return the symmetry to bilaterality. The ascarid worms belonging to the genera Polydelphis and Ophidascaris possess a dorsal lip which is smaller than the ventral ones, and further *Ascaridia columbae* Gmelin shows this peculiarity in particular. It has in addition developed two very large lateral cephalic alae rising at the base of the insertion of the subventral lips and extending as far as the two pedunculated subsymmetrical cervical papillae. The condition of the dorsal lip in such cases seems to indicate that further reduction leads to complete loss of the upper pharyngeal sector or cephalic sector, according to Seurat, as seen in the following genera: Protospirura, Hartertia and Acuaria. *Protospirura labiodentata* Hall (Fig. 31) and *Protospirura ascaroidea* Hall illustrate this condition much better than *Protospirura muris* in which the lips have been deeply cleft appearing, except for the bilateral arrangement, as six separate lips, although their basal regions are partly united by cuticula (Fig. 10).

Undoubtedly a similar condition is present in the family Gnathostomidae whose genera are characterized by two large tri-lobed lateral lips with the cuticula on their inner surfaces thickened and usually raised into tooth-like ridges which meet or interlock with those of the other lips. A curious feature of most of the members of the family is the possession of a head-bulb or cuticular swelling just behind the lips. This bulb contains four submedian, subglobular, membranous structures, the so called "ballonets," each of which is connected by one of the four cervical glands or cervical sacs. The apparent function of these glands seems to be to swell out the ballonets after the nematode has buried its head in the tissue and in this way, with the aid of the interlocking lips, the worm assures itself of a tight hold upon the host organ. The head-bulb may be coarsely striated

or beset with chitinous rose-thorn hooks with their roots buried well in the cuticula; for example *Tanqua tiara* von Linstow (Fig. 25) has five notched lips and coarsely striated cuticula, while *Gnathostoma spingerum* Owen (Fig. 34) has less elaborate lips and a spine beset collar. These forms live with few exceptions within the digestive tract of various animals. Their symmetry is undeniably bilateral as is that of the forms cited in the previous paragraph, and seems to have arisen by loss of the dorsal cephalic sector. In view of the fact that they also show a considerable specialization in the reproductive organs as well as in the cephalic region, one may say that this secondary return to fundamental bilaterality from the apparent radial symmetry of the three lipped forms agrees with the same condition found among the free living nematodes, as has already been demonstrated.

In connection with bilateral disymmetry there are quite a number of forms which would fall into the class of individuals with trisymmetrical cephalic regions if it were not for the development of two very pronounced median lateral anterior alae or the distinctly bilateral arrangement of papillae (*Spiroptera papillosa* Molin, *S. turdi* Molin and *Oxyuris obesa* Diesing, for papillae and *O. tetraptera* von Linstow, for alae). The Camallanidae are conspicuous for their lateral jaws. These consist of two valves similar in shape to Pecten or scallop shells, brownish in color and free only along the dorsal and ventral edges of the anterior halves. Throughout the other half they are fused so that cross sections exhibit a more or less oval chitinous ring. The interior surfaces are ridged and the exterior is covered by a delicate layer of cuticula. Another distinguishing feature of these nematodes is the pair of chitinous tridents, one dorsal and one ventral, articulating with the valves. This type of oral structure is apparently derived from a lip-like structure according to Magath, and Raillet and Henry (1915) have placed the Camallanidae under Spiruroidea, a group which is characterized by lateral lips. As the lateral disymmetry has in other spirurids arisen from loss of the dorsal cephalic sector, the same loss may be responsible for the formation of jaws in Camallanus, as is clearly the case among the free living nematodes already referred to as possessing bilateral jaws or mandibles.

Another oral organization which very closely resembles jaws in appearance and apparent function also is to be found in the genus Kalicephalus and perhaps less distinctly in Diaphanocephalus, both bursate nematodes of unsettled classification as yet, but according to Stossich apparently belonging to the Sclerostomes. The mouth capsule of *Diaphanocephalus costatus* Diesing is transparent and armed or strengthened by eight cuticular or chitinous ribs running vertically and between these buried deep in the capsule are six papillae. The striking feature of the capsule is that the buccal orifice in place of being circular is a spindle-shaped opening as if the edges of the capsule had been compressed and approximated laterally.

This condition is still more apparent in *Kalicephalus inernus* Molin (Fig. 20) where the capsule is rather more compressed and the appearance of jaws accentuated. The supporting ribs are united anteriorly but are separated posteriad. The exact genesis and significance of this disymmetry and of the jaws in Camallanus cannot be known until the larval developments have been carefully examined, but from adult features their similarity cannot be structurally the same.

Turning now to a consideration of parasitic forms which possess cephalic structures arising from a variation of numbers of lips particularly other than three, one finds interesting indications of fusion and capsule formation. The lack of larval and embryological studies on most nematodes makes the problem rather difficult, but as this evidence is unobtainable, conclusions must be based on adult structures. However, as a matter of fact, Seurat has shown in his studies on larval forms that many features of the young do not differ strikingly from those of the adult. The general cephalic structure is often the same, giving little information regarding its evolution. The reproductive systems, however, have been chosen as showing the most phylogenetic facts. Furthermore, in larval comparisons care must be taken to distinguish between structures of apparent phylogenetic importance and those cenogenetic in nature.

Among the oxyurids there are three lipped forms (*O. obvelata*), six lipped ones (*O. hydroi* Galeb), and some with a capsule apparently arising from a fusion of lips (*O. obesa* Diesing and *O. equi* Schrank), and there is even a two-lipped species (*O. monhystera* von Linstow). It is open to question, however, whether the two lipped and capsulated forms are true oxyurids and whether such a diversity of form might not better indicate a generic rather than a specific relationship.

In the family Filaridae the members are characterized partially by their lack of cephalic armature. No pharynx is present; the head is usually rounded with circular mouth opening and with few exceptions no lips are present although cephalic papillae may be apparent existing in the numbers of four and six. Such details would naturally be expected among forms reduced to such a degree of parasitism as these nematodes are. *Filaria bancrofti* Cobbold, for example, has an unarmed circular mouth and two circlets of six low inconspicuous cephalic papillae while *F. candezei* Seurat is similarly constructed except that the second circlet of papillae contains only four. *Acanthocheilonema diacantha* from the body cavity and lungs of various Brazilian rodents possesses a circlet of six papillae of which the median lateral ones are very large, giving the head a square outline in dorsal or ventral view. A curious feature of the head region of members of the filarid genus Diplotriaena (*D. diucæ* Boulenger) is the occurrence of two lateral chitinous tridents reminiscent of those in Camallanus except that in this latter genus they are dorsal and ventral tridents in connection with the lateral valves.

A slight modification of the filarid head suggesting the possibility of two lateral lips is found in *Setaria equina* Abildgaard, where the mouth is surrounded by a chitinous ring, the lateral portions of which are projected as two semilunar lips. There is as well on the dorsal as the ventral surface a papilliform process and at a lower level on the head there are four submedian prominent papillae. In all the filarid worms just mentioned, with perhaps the exception of the first, the symmetry is bilateral, chiefly so on account of the hypertrophy of the lateral papillae or because of the presence of four submedian in place of six radially placed papillae.

A very noticeable case of radial cephalic symmetry exists in *Spirocera subaequalis* Molin (Figs. 24 and 32) in the adult form. The six denticles of the two lateral lips are regularly disposed around one axis and the buccal border is cut into six equal lobes. This radial symmetry is, however, secondary because in the larval stages of this particular worm, the symmetry is bilateral till the nematode has passed into the fourth larval stage.

In the genera Eustrongylides and Hystrichis, the mouth is usually a triangular or circular opening leading into a very short vestibule similarly shaped in cross section. The buccal aperture is surrounded by six papillae on very prominent projections which have a slight tendency to bilateral arrangement although the radial appearance is more striking. *Hystrichis acanthocephalicus* Molin illustrates this characteristic quite well (Fig. 29). Species of Eustrongylides possess in addition to the six large papillae six to twelve smaller ones, as *E. elegans* von Olfers (Fig. 36).

Finally in the strongylids one finds the most interesting of oral developments in the form of a large armoured buccal cavity or pharynx. The oral aperture is directed often dorsally as in the hookworms or terminally as in the sclerostomes, but of these positions the dorsal location is purely a secondarily acquired one, occurring late in the larval life. *Ancylostoma duodenale* Dubini illustrates very admirably the general plan of such cephalic parts. The ventral margin of the mouth which projects farthest forward carries on each side of the middle line a pair of strong teeth with backward bent prongs. The outer one is always larger and the inner one has near its base on the side turned toward the median plane of the body a small accessory tooth. The dorsal edge of the capsule shows in the middle line a short and rather deep incision of which only the two anterior angles project above the rim, because the greater part of this structure is covered by the cuticula. Upon the ventral wall of the mouth capsule near the base of the cavity is another pair of saw-like teeth projecting freely into the cavity and converging backward only slightly. The dorsal wall of the cavity is pierced obliquely from without inward by the excretory duct of the dorsal esophageal gland.

The whole mouth capsule is one continuous chitinous piece of material which, however, can be changed slightly in shape through the presence in its walls of several sutures where the hard parts are so thin as to permit a

small degree of movement. Internally the capsule is lined by a delicate membrane through which the teeth project from the capsule wall while externally there is a covering of granular material and the cuticula. When variations of this capsular structure arise, it is mainly in the change of form among the teeth and cutting plates. The papillae are six, arranged bilaterally near the edge of the capsule with three on each side (*Ancylostoma caninum* Ercolani Fig. 40).

The head of the larva of the above form is radially symmetrical regarding the triquetrous mouth opening and the papillary arrangement, two to each sector, however the presence of two mid-lateral ridges alters the symmetry to the same as exists in the adult. Indeed, none other than bilaterality could exist in such a structure as the adult capsule. The question of the origin of the capsule can be only partly answered from the larval forms. In the young free-living larva the pharynx is a rather long unarmed tube entered apparently by the triquetrous opening between the three fused lips. If this interpretation is correct, then the buccal capsule arises from a fusion of lips in connection with a large pharynx, as is the case with some of the free-living forms (Figs. 18, 19, 23).

In contrast to the hookworm capsule is the type found among the Sclerostomes which have the mouth opening anteriorly terminal. The general anatomy of the cephalic region is the following: the cuticula or skin is considerably thickened around the edge of the mouth and constricted by a groove which produces a fold of cuticula, the mouth collar. The anterior edge of this structure becomes split up into a very characteristic and delicate fringe which Looss calls the "external leaf crown" the base of which rests on the edge of the buccal capsule. There are six cephalic papillae disposed radially and equally distant from each other. They do, however, shift at times and assume a bilateral arrangement. The medial lateral ones are slightly different from the other four rather submedial papillae which possess cuticular points. The capsule is formed of a homogeneous substance lined by a delicate granular membrane and along the mid-dorsal wall runs the gutter or duct of the dorsal esophageal gland, while at the base on either side there may be two rounded inward pointing plates opposed by two similar ones on the ventral side (*Sclerostomum equinum* Müller) (Fig. 39). These both, however, may be absent or in other genera replaced by three three-flanged teeth arising symmetrically from the floor of the capsule (*Triodontophorus minor* Looss) (Figs. 26 and 38).

The symmetry of the former specimen could not be other than bilateral but of the latter, were it not for the dorsal gutter and a few minor external details, the symmetry would superficially pass as radial. As in previous forms, the striking specific differences arise from modifications of the "leaf-collar," of the general outline of the capsule, and of the armatures arising from the floor and walls of the buccal cavity, but at no time is the symmetry radial in the sense of including other than the most superficial details.

CILIATION AMONG NEMATODES

Former Views and Present Data

It has been a generally held view that nematodes in company with arthropods form the two animal groups totally devoid of cilia at any stage in their existence. Fasten, however, disproved the opinion for arthropods by demonstrating cilia as being present in the reproductive ducts. Shipley in remarking upon the absence of cilia in these two groups believes the condition is correlated with the tendency to form cuticula among nematodes and with the great proclivity for chitinization in arthropods This view is possibly correct as appears when one examines the variations of intestinal linings among different species of nematodes.

Prenant, who has made a special study of cilia and ciliary modifications, has recently placed in the category of "bordure en brosse" the characteristic intestinal lining of *Ascaris megalocephala*. An examination of one of his original preparations of the sectioned intestine of this ascarid, showed the lumen-ward end of the cells covered by a thick, rather finely striated border. The elements, however, composing this border are not separately distinguishable for the whole lining is a unit. Just beneath this border is a distinct row of darkly staining basal granules which, too, are more or less confluent and followed by a relatively deep homogeneous zone. This latter portion gives way to the subcentral granular zone through the middle of which is a relatively clear space. The nuclei are basal and lie in a region containing numerous filaments running the long way of the cell. Other authors in treating of this border have pictured the same condition but called it either a cuticular border or a "Stäbchensaum."

Looss found a similar striated border upon the intestinal cells of *Ancylostoma duodenale* but in the cases where individual rods or elements were visible and separate he attributed them to a degeneration of the border, as such were usually seen in adult worms, the younger specimens exhibiting a more united and homogeneous appearance. Such a feature is, no doubt, due partly to the fixation of the material as will be shown later. Martini shows in his studies upon *Oxyuris curvula* identical structures in the intestinal cells (Figs. 46 and 47) and calls the lining a "Stäbchenbesatz." In an alcohol preparation the "Stäbchen" are not clearly separated but in another, a gold chloride one, the lumen ends are apparently free. Following the border is an indistinct layer of basal granules from which fibrils may be traced rather indistinctly into the body of the cell proper. Rauther also in working upon Enoplus describes the intestinal

cells as covered by a "Stäbchensaum" (Fig. 43). In his illustration the distinctness of the striae is unmistakable and a splendid basal granule layer is present where each granule is identifiable as well as the fibres running from them into the cell itself.

Another example of apparent ciliation is to be found in *Ichthyonema pellucidum* in the intestinal canal (Fig. 44). Jägerskiöld in describing it states that the lining of this material did not resemble the "Stäbchenlage" of most nematodes because the little rods were widely separated and quite long. He did not, however, examine any fresh material and concludes, "so glaube ich night fehlzugreifen, wenn ich es als eine eigenthümlich ausgebildete Stäbchenlage und nicht als ein Wimperkleid betrachte."

An interesting feature of these "bordures en brosse" is that only one author has seen any vibratile motion in the cilia. Cobb (1898) makes this statement: "Toward the end of the seminal vessel, near the ejaculatory duct, the epithelium bears projections having amoeboid movements or cilia having active vibratile motions. This latter interesting fact, first made known by the observer, is of special importance as being the first discovery of a ciliated epithelium among nematodes, a tissue which had been supposed not to exist in the group, and the supposed absence of which had given rise to phylogenetic speculations." He does not, however, present any drawings or name the species in which such a condition occurs and offers no other data in any later papers.

During some observations upon *Protospirura muris*, the author was particularly struck by the apparent beautiful ciliation of the intestinal cells as they appeared in sections prepared from material killed in Carnoy-phenol. Previous examination of sections from specimens killed by Looss' method, showed a more or less hyaline structureless intestinal lining broken into bristle-like portions here and there which, since they were found in mature specimens, were interpreted as degenerating portions of the cuticular lining as Looss had previously interpreted that structure in *Ancylostoma duodenale*. More material was killed in Flemming's mixture without acetic acid and sectioned. The cells exhibited the same discrete ciliation which, too, was present in a very young specimen fixed previous to its last moult. This latter fact indicates that the condition is not due to the age of the specimen.

For further proof of the ciliary nature some fresh, living nematodes were collected and the intestine examined immediately in normal salt solution under dark field illumination and oil immersion. The individual cilia could very plainly be seen in both cases but no motion of their own was ever noted. They would, however, wave back and forth in response to currents of water flowing through the intestine when the slightest pressure shifted the coverglass. The fact that no motion was visible may have been due not to a lack of power of the cilia to beat but to a lack of suitable

temperature conditions or to the absence of calcium salts from the isotonic saline used as an examination fluid—a point not fully appreciated at the time of observation.

In sections (Fig. 45) stained with Dobell's iron hematein one may distinguish the long cilia, an indistinct, rather fused row of basal granules and the fibrils extending into the cell body. Usually the middle portion of the cell is very granular and at times alveolar in appearance so the fibrils disappear but sometimes reappear in the region of the nucleus. Such cells are structurally identical with other ciliated cells and differ physiologically only in the lack of motile cilia.

Significance of Ciliation

From a morphological point of view this loss of motion and graded fusion of cilia indicate a retrogression and an atrophy because the divers parts constituting the vibratile apparatus become less and less evident until they are finally obliterated; but from a physiological point of view, this regression, when it is a case of differentiation, is a step in advance, for there results the formation of new organs with new functions. In the case of nematodes the possession of cilia, though they be immotile, is best construed as a hang-over from a more primitive condition of active ciliation. This being the case, the way is open for phylogenetic speculations and a still closer possible relationship can exist then between the nematodes and the rotifers and gastrotricha to which the roundworms at present seem most closely related.

With a ciliated alimentary tract throughout, as rotifers have at present, the ancestral nematode would necessarily have had no need of a muscular sucking esophagus or lips or pharynges. A simple circular mouth in that case would be the most logical form, such as many of the rotifers possess. Perhaps then the very structureless mouth region of some of the simpler marine nematodes mentioned in the fore part of this paper shows the most primitive form of oral structure, i.e. circular mouth, no lips, indistinct papillae and no pharynx, in contradistinction to the three lipped form described by Seurat as the most primitive condition of oral structure. Loss of ciliation may have arisen by the propensity for cuticularization and by some other unknown change or cause, the simple ciliate esophagus became a muscular sucking organ to carry on the process of acquiring food after ciliary motility had given place to non-motility as evinced by the "bordures en brosse" of species today.

DISCUSSION AND CONCLUSIONS

Regarding orientation of the primitive nematode with respect to its surroundings, Steiner's view that it maintained a position perpendicular to the substrate and followed the half-sessile mode of life seems to be tenable and is well borne out by many of the free-living forms found on and about marine algae and particularly by those worms possessing eye spots with the lenses vertically oriented. The crawling mode of travel engaged in by many nematodes as they lie upon a lateral surface is a secondarily acquired mode of locomotion. Furthermore, the vertical orientation suggests that possibly the ancestor of the nematode, in view of cilia being present, was a free swimming pelagic elongate animal which, after assuming the tendency to cuticularize, settled down to a half-sessile life. The ancestral mouth in the stage with the ciliated digestive tract was possibly ventral and circular, opening into a ciliated esophagus, only slightly muscular or not at all so, and in all probability the anus of such an individual was terminal as well also as the openings of the excretory system. This view is in accord with single openings of these systems spoken of by Seurat in the definition of the primitive nematode. Such an ancestor might easily be derived from a trochophore form by extensive elongation and a partial migration of the mouth anteriad. Further the symmetry of such an individual would be bilateral which is of course in accord with the fundamental bilaterality of the nematode.

The limiting descriptions of the structural units, lips, jaws, and capsule, proposed by Ward primarily for the parasitic nematodes, are equally applicable to free-living forms, but here there are intergradations from one form to the other so that as a means of grouping the free-living roundworms, these terms are too restrictive and do not permit of placing many intermediate conditions.

From the foregoing discussion and the data in the preceding sections, the following conclusions may be drawn:

1. Cilia are present in nematodes in modified forms and as discrete elements structurally identical with those of vibratile ciliated cells.
2. The nematode ancestor was probably ciliated throughout its digestive tract, and possessed perhaps external cilia, a ventral, simple mouth, and a terminal anus.
3. Loss of external ciliation was succeeded by a half-sessile life and tendency toward cuticularization. The muscular esophagus arose as a pumping organ.

4. The fundamental symmetry is bilateral. True radial symmetry is rare but apparent radial symmetry is very noticeable in the cephalic region and is a secondary condition resulting primarily from the sessile tendency.
5. Disymmetry is tertiary as is asymmetry.
6. The simplest and perhaps most primitive cephalic organization was and is in some forms today, a round or triquetrous mouth opening directly into the triquetrous esophagus, with small or indistinct oral papillae. Successive complication and evolution of structure may be thought of as taking place in the following order:
   (a) Three lipped forms with no pharynx.
   (b) Three lipped forms with developing pharynx.
      (1) Two-lipped forms with no pharynx arising from loss of the dorsal lip.
      (2) Jaws arising from loss of upper or dorsal cephalic sector and migration laterally of the two subventral sectors.
   (c) Multiple lips by division of the primitive number.
   (d) Partial fusion of multiple lips and development of large armed pharynges.
   (e) Capsule formed by fusion of lips in connection with a large pharynx armed generally by strong onchi.
      (1) Spear-bearing forms from fusion of lips, elongation of pharynx, and fusion and separation of onchi from the pharyngeal walls to form the buccal stylet moved by special muscles.
7. Disymmetry is more noticeable among parasitic forms than among free-living forms.
8. Cephalic organization has kept pace with other specializations and bears a relation to habitat and is indicative in a general way of the evolutionary status of a genus.

LIST OF FREE-LIVING SPECIES CITED

	PAGE
Alaimella cincta Cobb	22
Alaimella truncata Cobb	22
Anaxonchium litorium Cobb	26
Bunonema inequale Cobb	16
Cephalobus ciliatus von Linstow	19, 25
Cheironchus torax Cobb	24, 28
Diploscapter coronatus Cobb	28
Dorylaimus labiatus de Man	28
Gammonema ferox Cobb	24
Heth juli Cobb	28
Ionema ocellatum Cobb	17, 22
Iotodorus punctatus Cobb	26
Litotes minuta Cobb	22
Mesonchium poriferum Cobb	23
Monhystera pilosa Cobb	17
Monhystera stenosoma de Man	23, 26, 27
Mononchus gerlachei de Man	21, 22
Mononchus muscorum Bastian	23
Mononchus radiatus Cobb	23
Mononchus zschokkei Menzel	23
Nemella ocellata Cobb	17
Notochaetosoma tenax Irwin-Smith	17
Onchullela ocellata Cobb	17
Pomponema mirabile Cobb	17, 26
Rhabditis lambdiensis Maupas	25
Rhabditis pellio Bütschli	25
Scaptrella cincta Cobb	14, 24
Selachinema ferox Cobb	28
Sphaerolaimus hirsutus Bastian	17
Spira parasitifera Bastian	18
Synonchium obtusum Cobb	24, 28
Teratocephalus crassidens de Man	25
Terschellingia longicaudata de Man	23
Thoracostoma autarcticum von Linstow	17
Thoracostoma lobatum Cobb	17
Thoracostoma setosum von Linstow	25
Tycnodora pachydermata Cobb	22
Tylopharynx stricta de Man	24
Wilsonema capitatum Cobb	28
Xyala striata Cobb	24

LIST OF PARASITIC SPECIES MENTIONED

	PAGE
Acanthocheilonema diacantha (Molin 1858) Boulenger 1920	36
Syn. *Filaria diacantha* Molin 1858 *Filaria loncheri* M. C. V. Molin 1858 *Filaria hystrichis-prehensilis* Molin 1858	
Ancylostoma duodenale Dubini 1843	37, 39, 40
Syn. *Ankylostoma duodeno-jejunale* (Dub. 1843) Leichtenstern 1886 *Ankylostoma hominis* (Poeppel 1897) Leichtenstern 1889	
Ascaris holoptera Rud. 1819	34
Ascaris nasuta Schneider 1866	34
Ascaris osculata Rud. 1802	34
Ascaris rosmari Baylis 1916	60
Syn. *Ascaris bicolor* Baird 1868	
Crossophorus collaris Hemprich and Ehrenberg	33
Diaphanocephalus costatus Diesing 1851	35
Syn. *Strongylus costatus* Rud. 1819 *Sclerostoma costatum* Dujardin 1845	
Diplotriaena diucae Boulenger 1920	36

PAGE

Dracunculus medinensis (Linn 1758) Gallandat 1773 14
Syn. *Vena medinensis* Velsch 1674
Dracunculus persarum Kaempfer 1694
Gordius medinensis Linnaeus 1758
Filaria medinensis (Linn. 1758) Gmelin 1790
Filaria dracunculus Bremser 1819
Filaria aethiopica Valenciennes 1856
Eustrongylides elegans (von Olfers 1816) Jägerskiöld 1909 37
Syn. *Strongylus papillosus* Rudolphi 1802
Strongylus mergorum Rudolphi 1809
Strongylus elegans von Olfers 1816
Strongylus tubifex Rudolphi 1819
Eustrongylus tubifex Diesing 1851
Hystrichis tubifex Molin 1861
Hystrichis elegans Raillet 1893
Hystrichis papillosus Molin 1861
Tropidocerca paradoxa von Linstow 1877
Eustrongylides ignotus Jägerskiöld 1909 33
Syn. *Eustrongylus papillosus* Diesing 1851
Eustrongylus tubifex (Nitzsch 1819) Schneider 1866
Hystrichis papillosus Molin 1861
Filaria bancrofti Cobbold 1877 36
Syn. *Trichina cystica* Salisbury 1868
Filaria sanguinis hominis Lewis 1872
Filaria nocturna Manson 1891
Filaria wüchereri da Silva Lima 1877
Gnathostoma spinigerum Owen 1836 35
Syn. *Chieracanthus robustus* Diesing 1839
Chieracanthus socialis Leidy 1858
Chieracanthus siamensis Levinsen 1890
Filaria radula Schneider 1866
Gnathostoma paronai Porta 1908
Gnathostoma spinigerum Mither 1912
Gongylonema musculi (Rud. 1819) Neuman 1894 32
Syn. *Gongylonema minimun* Molin 1857
Filaria musculi Rudolphi 1819
Hystrichis acanthocephalicus Molin 1861 37
Heterodera schachtii Schmidt 1871 ..... 14, 15
Kalicephalus inermis Molin 1861 36
Syn. *Strongylus colubri-jararaca* M. C. V.
Strongylus crotali M. C. V.
Ophidascaris mombasica Baylis 1920 34
Oxyuris equi (Schrank 1788) E. Blanchard 1849 ..... 7, 36, 39
Syn. *Oxyuris curvula* Rudolphi 1803
Oxyuris hydroi Galeb 1878 36
Oxyuris monhystera von Linstow 1902 36
Oxyuris obesa Diesing 1851 ..... 35, 36
Oxyuris obvelata (Rud. 1802) Dujardin 1845 ..... 21, 36
Syn. *Ascaris vermicularis muris* Fröelich 1791
Ascaris obvelata Rud. 1802
Fusaria obvelata Zeder 1803
Ascaris oxyura Nitzsch 1821
Syphacia obvelata (Rud. 1802) Seurat 1916

PAGE
Oxyuris tetraptera (Nitzsch 1821) von Linstow 1878 ..... 32, 35
Syn. *Ascaris dipodis* Rud. 1819
Oxyuris semilanceolata Molin 1858
Oxyuris obvelata Dujardin 1845
Polydelphis quadricornis (Wedl 1862) Baylis 1920 34
Syn. *Ascaris quadricornis* Wedl 1861
? *Ascaris quadrangularis* Schneider 1866
? *Ascaris quadrilobata* von Linstow 1908
Protospirura ascaroidea Hall 1916 34
Protospirura labiodentata (von Linstow 1899) Hall 1916 34
Syn. *Spiroptera labiodentata* von Linstow 1899
Protospirura muris (Gmelin 1790) Seurat 1915 ..... 21, 32, 33, 34, 40
Syn. *Lumbrici muris* Werner 1782
Lumbricus muris Rud. 1809
Ascaris muris Gmelin 1790
Ascaris obtusa Froelich 1791
Fusaria muris Zeder 1803
Spiroptera obtusa Rud. 1819
Filaria muris Stossich 1897
Spiroptera brauni von Linstow 1871
Sclerostoma equinum (Mueller 1784) Blainville 1828 38
Syn. *Strongylus armatus* Rud. 1802
Strongylus neglectus Poeppel 1897
Setaria equina (Abildgaard 1784) Raillet & Henry 1911 37
Spirocera subaequalis (Molin 1860) Seurat 1913 37
Tanqua tiara (von Linstow 1879) Baylis 1916 35
Syn. *Ascaris tiara* von Linstow 1879
Ctenocephalus tiara (von Linstow 1879) von Linstow 1904
Tetradenas tiara (von Linstow 1879) von Linstow 1904
Trichosomoides crassicauda (Bellingham 1845) Raillet 1895 ..... 15, 21
Syn. *Trichosoma crassicauda* Bell 1840
Trichocephalus crassicauda Eberth 1863
Trichodes crassicauda von Linstow 1874
Trichosoma muris-decumani Bayer & Stossich 1843
Triodontophorus minor Looss 1901 38

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PLATE I

EXPLANATION OF PLATES

Plate I

Fig. 1. *Oxyuris obvelata.* Head of a female en face showing the 3 lips and the 6 papillae disymmetrically arranged. After Flögel. ×650.

Fig. 2. *Teratocephalus crassidens.* Lateral view showing the peculiar flanged lips. After de Man. ×220.

Fig. 3. *Mononchus gerlachei.* Head en face showing the 6 partially fused lips, the pharyngeal armature, the large dorsal tooth and the superficial radial symmetry. After de Man. ×600.

Fig. 4. Same as in Fig. 2, dorsal view. After de Man. ×220.

Fig. 5. *Anguillula aceti.* Head of female en face, showing fused lips and hexagonal mouth opening. After de Man. ×1250.

Fig. 6. *Cephalobus ciliatus.* Showing the peculiar prolongations of the lips. After de Man. ×220.

Fig. 7. Jointed mandibles of *Scaptrella cincta* inflexed and extended. After Cobb. ×550.

Fig. 8. Optical cross section of the posterior portion of buccal cavity of a growing female, *Anguillula aceti.* After de Man. ×1900.

Fig. 9. Cross section of pharynx of *Mononchus muscorum* showing the sutures and the dorsal tooth. After Cobb. ×400.

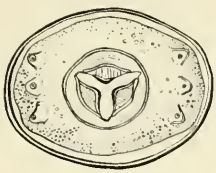
Fig. 10. Head of *Protospirura muris* showing the disymmetry of the two tri-partite lips. Original ×200.

Fig. 11. Jointed cephalic seta. After Cobb.

Fig. 12. Lateral optical section of *Monochus macrostoma,* showing spacious pharynx and large dorsal tooth. After Cobb. ×400.

Fig. 13. Head of *Monhystera pilosa* showing the delicate cephalic bristles. After Cobb.

Fig. 14. Head of a growing female of *Anguillula aceti,* showing the break in the pharyngeal wall between upper and lower sections. After de Man. ×1250.



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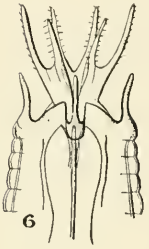

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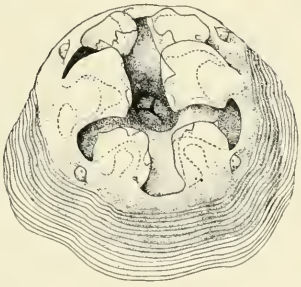

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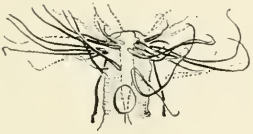

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14

HETHERINGTON STUDIES ON NEMATODES PLATE I

PLATE II

PLATE II

Fig. 15. *Crossophorus collaris*. Dorsal view showing the fimbriae and the two symmetrically placed papillae of the dorsal lip. After Bayliss and Lane. ×60.

Fig. 16. *Synapticulum mirabile*, showing the six double continent lips, the fusing triquetrous pharynx and its armature of mandibles. After Cobb. ×400.

Fig. 17. *Polygordius triestinus*, showing true radial symmetry. After Bayliss. ×130.

Fig. 18. *Amphioxus lanceolatus*. Larval head, viewed en face, showing the triquetrous mouth opening, the three fused lips and six papillae. After Looss. ×300.

Fig. 19. *Amphioxus lanceolatus*. Larval head, dorsal view, showing pharynx. After Looss. ×330.

Fig. 20. *Kalicephalus vitiyi*. Front view of head showing the lateral approximation of the cuspular edges. After von Linstow.

Fig. 21. *Thwaitesinus chilensis*. Dorsal view of the oesophagus showing the two ocelli with the ventrally directed lenses. After Steiner. ×370.

Fig. 22. *Thwaitesinus acuticaudatus*, showing the serial arrangement of the cranial glands. After Jägerskiöld. ×80.

Fig. 23. *Amphioxus lanceolatus*. Larval head, lateral view, showing the tubular pharynx. After Looss. ×330.

Fig. 24. *Spironora subequalis*, showing the radial symmetry of the oral region. After Seurat. ×120.

Fig. 25. *Fungus lives*, showing the collar and the two lateral lips. Dorsal or ventral view. After Bayliss and Lane. ×110.

Fig. 26. *Trichonotophorus minor*, showing the terminal mouth and the three pharyngeal teeth in front view. After Looss. ×80.

Fig. 27. *Kalicephalus trilongis*. Head en face, showing the apparent radial symmetry and the large interlabia. After Gedoelst.

Fig. 28. *Crossophorus collaris*. Diagrammatic representation of lip and fimbriae relations and symmetry. After Bayliss and Lane.

Fig. 29. *Heterakis acanthocephalicus*, showing the spine beset head and the simple triquetrous mouth with six circumoral papillae. After Jägerskiöld. ×80.

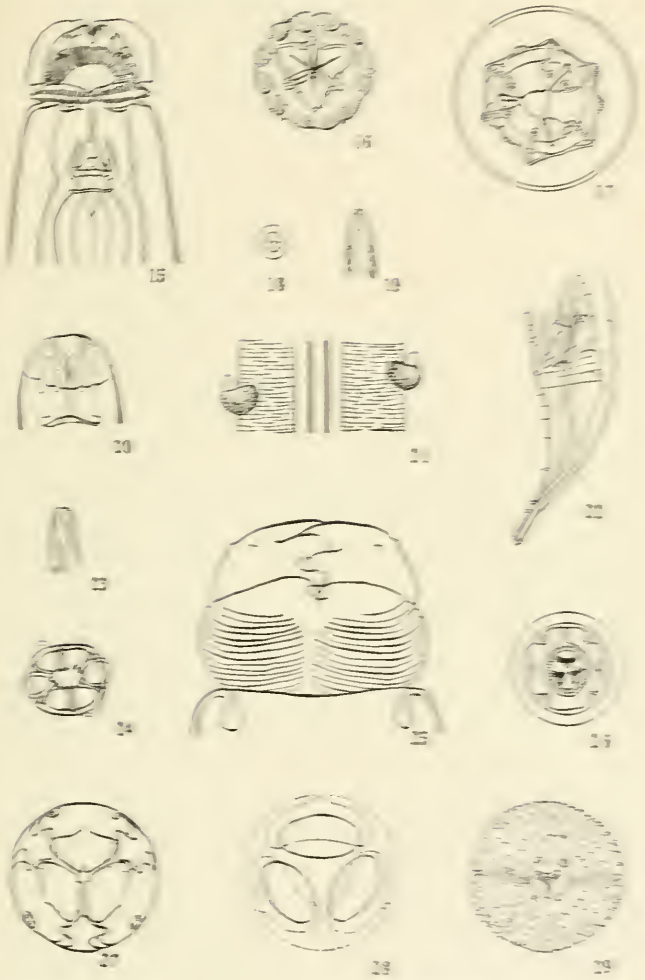
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PLATE III

PLATE III

Fig. 30. *Thoracostoma chilensis*. Lateral view of head showing the location of an ocellus. After Steiner. ×370.

Fig. 31. *Protospirura labiodentata*. View en face showing the two tripartite lateral lips and the disymmetrically arranged papillae. After von Linstow.

Fig. 32. *Spirocera subaequalis*, showing the buccal armature. See figure 24. After Seurat. ×50.

Fig. 33. *Camallanus americanus*. Dorsal view of the oral apparatus of a female showing the two lateral valves and the dorsal trident. After Magath. ×80.

Fig. 34. *Gnathostoma spinigerum*, dorsal view, showing the two lateral lips and the spine beset head. After Baylis and Lane. ×40.

Fig. 35. *Kathleena arcuata*. Head en face showing the apparent triradial symmetry and large interlabia. After Gedoelst.

Fig. 36. *Eustrongilides elegans*, showing the prominent papillae and the slight tendency toward disymmetrical arrangement. After Jägerskiöld. ×40.

Fig. 37. *Ascaris ferox* (*Crossophorus collaris*). Lateral lip showing the asymmetrical arrangement of papillae. After Schneider. ×45.

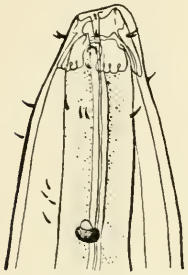
Fig. 38. *Triodontophorus minor*, lateral view, showing the three pharyngeal teeth. After Looss. ×80.

Fig. 39. *Sclerostomum equinum*, dorsal view, showing the "leaf-crown," dorsal gutter and the large buccal cavity. After Looss. ×30.

Fig. 40. *Ancylostoma caninum*, showing the ventral teeth and capsule. After Looss. ×100.

Fig. 41. *Kathleena tricuspis*. Head, dorsal view, showing the interlabia. After Gedoelst.

Fig. 42. *Ascaris rosmari*. Lips, viewed en face, showing the large dorsal lip. After Baylis. ×90.



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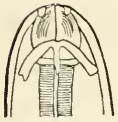

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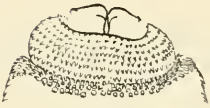

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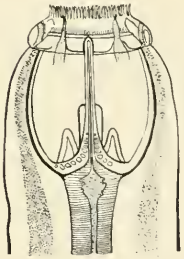

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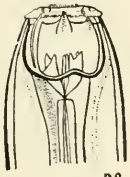

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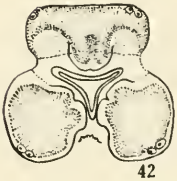

42

PLATE IV

PLATE IV

Fig. 43. *Enoplus sp.* Section of the intestinal wall showing the ciliated border with its basal granules and their fibrillar continuations. After Rauther. ×1440.

Fig. 44. *Icthyonema pellucidum.* Section of the intestinal wall showing the separated ciliary structures. Enlarged after Jägerskiöld.

Fig. 45. *Protospirura muris.* Section of the intestinal wall showing two cells with their long cilia, rather indistinct basal granules and their fibrillar prolongations into the cytoplasm. The dark bodies within the clear spaces are areas infected with *Thelohania reniformis* Kudo and Hetherington, a microsporidian parasite. Original. ×2100.

Fig. 46. *Oxyuris curvula.* Gold chloride preparation of an intestinal cell showing the ciliary structures. Enlarged after Martini.

Fig. 47. Same as above. Alcohol preparation showing the "Stäbchensaum." Enlarged after Martini.

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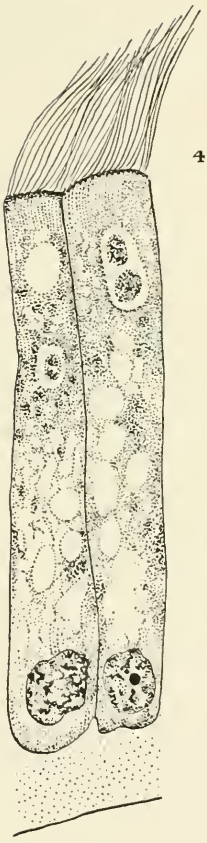
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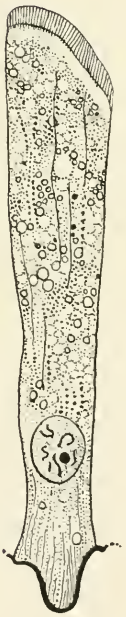
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46

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PARASITIC FUNGI FROM BRITISH GUIANA AND TRINIDAD

WITH NINETEEN PLATES AND A MAP IN THE TEXT

BY

FRANK LINCOLN STEVENS

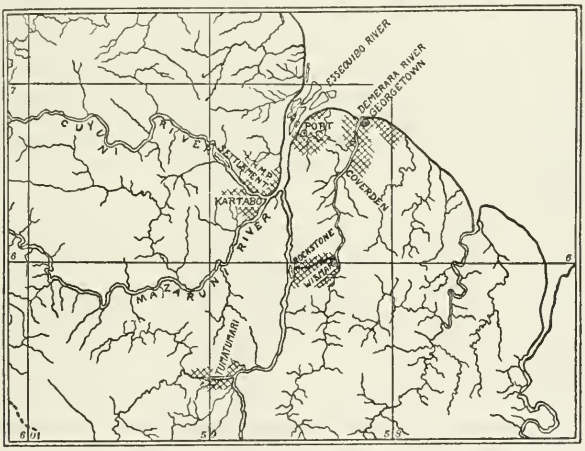
Contribution from the
Botanical Laboratories of the University of Illinois

TABLE OF CONTENTS

Introduction 7
Polystomellaceae 10
Parmulineae 10
Hysterostromina 10
Dothideaceae 10
Coccoideae 10
Coccostromopsis 10
Nowellia 11
Leveillelleae 13
Leveillinopsis 13
Dothideae 13
Bagnisiopsis 13
Amerodothis 14
Uleodothis 15
Achorella 15
Phyllachoraceae 16
Scirrhiineae 16
Anisochora 16
Scolecodothopsis 17
Phyllachorineae 18
Phyllachora 18
Endodothella 24
Montagnellaceae 25
Eu-Montagnelleae 25
Haplothecium 25
Hemisphaeriaceae 25
Gymnopeltis 25
Perisporiaceae 26
Dimeriella 26
Phaeodimeriella 27
Meliolinopsis 27
Hyalomeliolina 27
Oplothecium 28
Haraea 29
Parodiopsis 29
Dimerium 31
Mycophaga 31
Perisporiaceae Imperfecti 32
Pycnodothis 32
Capnodiaceae 32
Polystomellopsis 32
Clypeosphaeriaceae 34
Stegastroma 34
Anthostomella 35
Explanation of plates 37
Index to species 75
Index to hosts 76

INTRODUCTION

The notes and descriptions presented herewith are based upon collections of parasitic fungi made by the author mainly in the jungle of British Guiana, during the summer of 1922. The collections are in no sense comprehensive since the period of time was brief and travel in the interior of the country was difficult and tedious which resulted only in a sampling of a small part of a very interesting territory. The collections were made from five centers in British Guiana; Georgetown, the Demerara-Essequibo railroad, Coverden, Tumatumari and Kartabo.



The region of Georgetown and extending for many miles inland is flat, but a few feet above sea level, and of rather monotonous flora including many grasses and littoral plants, with trees bordering the rivers.

The Demerara-Essequibo railroad, 18½ miles long, extending from Wismar, which is 65 mi. inland on the Demerara river, to Rockstone on the Essequibo crosses a sandy upland from which the original forest has been cut, but which gives considerable diversification of flora. Especially at Wismar and at Rockstone where the sand hill flora merges with that of the river bank is the collecting excellent.

Coverden on the bank of the Demerara about 20 mi. from the sea gives a few isolated sand hills covered with the original forest growth of great diversification which differs essentially from that found elsewhere.

Tumatumari on the Potaro River about 150 mi. inland is in the foothills surrounded by tropical jungle which may be traversed for many miles on foot by way of cut trails.

Kartabo, the temporary location of Dr. Beebe's laboratory, on the point formed by the junction of the Mazaruni and the Cayuni rivers, and only a few miles from the junction of the Essequibo is also in primitive jungle. All of these localities, except that of Georgetown, are without apparent influence of man on the flora, and its wilderness is evidenced by the sight at any moment of tapirs, peccaries, monkeys, deer, ant eaters, or possibly a boa constrictor.

The itinerary included also a few days collecting in Trinidad confined chiefly to the immediate vicinity of the Port of Spain, St. Augustine, Cumuto and The Long Stretch.

Practically no collections or records have previously been made of the parasitic fungi of British Guiana. Though my collections can be regarded only as a mere sampling they reveal a very rich fungous flora, especially rich in the Dothideales, Sooty Molds, Microthyriaceae and with a considerable abundance of rusts. The smuts are very scarce and the imperfect fungi, Phyllosticta, Cercospora, etc., are apparently less common than in the temperate region.

The summer's collection consisted of approximately a thousandnumbers, only certain families of which are reported in this paper; the genus Meliola, the Microthyriaceae, most of the Hemisphaeriaceae, the Trichopeltaceae being reserved. The slides, notes, original drawings and specimens on which these studies are based are deposited in the herbarium of the University of Illinois and duplicate specimens in the New York Botanical Garden. The photographs reproduced in the plates were made by A. G. Eldredge; the line drawings by L. R. Tehon.

The arrangement and classification of the Dothideales followed in this article is adapted from that of Theissen and Sydow[1] and, in so far as concerns the genera herein reported, is shown in the table of contents.

The following is a list of the field numbers with places and dates of collection.

		Date
TRINIDAD		
Nos. 1 to 8	Port of Spain	June 28
BRITISH GUIANA		
Nos. 9 –18	Georgetown	July 2

[1] Theissen, F. and Sydow, H., Die Dothideales. Ann. Myc., 13:149-746, 1915, and Synoptische Tafeln., Ann. Myc., 15:389, 1917.

Nos. 18 –22	Georgetown	July 4
Nos. 22 –30	Peters Hall	July 5
Nos. 30 –69	Tumatumari	July 8
Nos. 69 –105	Tumatumari	July 9
Nos. 105–154	Tumatumari	July 10
Nos. 154–215	Tumatumari	July 11
Nos. 215–248	Tumatumari	July 12
Nos. 248–262	Rockstone	July 13
Nos. 262–329	Wismar	July 14
Nos. 329–418	Demerara-Rockstone R. R.	July 15
Nos. 418–444	Rockstone	July 16
Nos. 444–495	Rockstone	July 17
Nos. 495–520	Kartabo	July 21
Nos. 520–575	Kartabo	July 22
Nos. 575–642	Kartabo	July 23
Nos. 642–681	Kartabo	July 24
Nos. 681–684	Penal Settlement	July 25
Nos. 684–707	Botanical Garden, Georgetown	July 31
Nos. 707–719	Georgetown, Lemada Canal	August 2
Nos. 719–720	Vreden Hoor	August 1
Nos. 720–746	Coverden	August 4
Nos. 746–758	Coverden	August 5
No. 758	Georgetown	August 6
Nos. 759–819	Coverden	August 8
TRINIDAD		
Nos. 819–821	Port of Spain	August 12
Nos. 821–848	St. Augustine	August 13
Nos. 848–856	Long Stretch	August 13
Nos. 856–875	Port of Spain	August 14
Nos. 875–901	St. Clair	August 15
Nos. 901–969	Cumuto	August 16
No. 969	Guanapo	August 16
No. 970	Port of Spain	August 26

POLYSTOMELLACEAE

PARMULINEAE

Hysterostomina Theiss. and Syd.

Ann. Myc., 13:228, 1915

1. Hysterostomina palmae Stevens n. sp.

[Figures 1 to 4]

Spots discolored, yellowed, showing from both leaf sides, bordering the stromata by a band several millimeters wide. Stromata radiate, epiphyllous, roughly circular, nearly entire, black, 2 to 4 mm. in diameter, superficial, but firmly attached. No free mycelium. Hypothecium well developed, extending deep into the mesophyll, brown, attached to the stromata by the whole of its base. Perithecia linear, irregularly arranged, 460μ in length, about 180μ wide, 110 to 145μ deep. Cleft 70 to 90μ wide, covering layer 18 to 25μ thick. Asci 8-spored, numerous; spores dark, 1-septate, 18 to 21 x 7μ, one cell darker and slightly larger than the other. Asci 43 to 45 x 18μ, thickened at the apex. Paraphyses numerous, filiform.

On Palm.

British Guiana: Tumatumari, July 12, 1922, *199*.

DOTHIDEACEAE

COCCOIDEAE

Coccostromopsis Plunkett n. gen.

Stroma prosenchymatic, without a definite covering layer, centrally attached, dothideoid. Loculi immersed, oval to spherical, equally distributed; asci clavate, 8-spored, paraphysate; spores continuous, elliptical, hyaline.

2. Coccostromopsis palmigena Plunkett n. sp.

[Figures 5, 6]

Stroma superficial, raised in irregular tubercles, brownish black, formed of perpendicular hyphae and attached by a central foot which penetrates into the mesophyll. Loculi sunken, oval to spherical, ostiolate, large, 250 to 400μ in diameter, without a wall; asci clavate, slightly stalked, 8-spored, arising basally and laterally in the loculi; 72 to 90; x 14 to 18μ; paraphyses hyaline, thin, filiform, 50 to 100 x 1.5 to 2μ; spores continuous, elliptical, hyaline, granular, inordinate, 18 to 21 x 5 to 7μ.

On leaves of palm, species indet.

Trinidad: Cumuto, August 16, 1922, *1001*.

The genus Coccostrompopsis differs from Coccostroma by having paraphyses; and from Auerswaldiella by having hyaline spores. The species described is somewhat similar to *Coccostroma palmigenum* (Berk. and Curt.) Theissen and Sydow[2] except for the presence of paraphyses. In the description of *Botryosphaeria palmigena* Berk. and Curt. cited by Theissen and Sydow was a synonym of *Coccostroma palmigenum*, paraphyses are described as being present. If this is true that fungus should not have been placed in the genus Coccostroma. The present species differs from that described as *Botryosphaeria palmigena* Berk. and Curt. in the size of spores and asci and in the absence of 4 and 6- spored asci. The presence of the paraphyses prevents the present species from being placed in Coccostroma and the hyaline spores keep it out of Auerswaldiella. I am inclined to believe that the material is not the same as that described as *Coccostroma palmigenum* (Berk. and Curt.) Theiss. and Syd. and, therefore, erect the new genus Coccostromopsis.

Nowellia Stevens n. gen.

Stroma Dothideaceous, superficial, centrally fastened to the hypostroma. Perithecia globular on the stroma. Asci with numerous paraphyses. Spores hyaline, 1-septate. Named in honor of W. Nowell of Trinidad in recognition of his researches on fungi.

3. Nowellia guianensis Stevens n. sp.

[Figures 7 to 14, 93.]

Superficial subiculum flat, thin, irregularly but distinctly radiate, without free mycelium, margin erose, 1to 3 mm., sometimes larger, in diameter, amphigenous but more abundant below. Stroma thick, centrally fastened to the hypostroma. Perithecia about 460μ high and almost equal diameter, globular, surface smooth or slightly rough, astomous and irregularly cracked, few (3 to 10) to many (100) on one subicle. Asci 90 to 100 x 11μ, clavate. Paraphyses numerous, filiform, gelatinous. Spores hyaline, 1-septate, enclosed in a gelatinous envelope, 22 x 55μ exclusive of the gelatinous envelope, thickest in the middle and tapering slightly toward the ends.

On unknown plant of the Celastraceae.

British Guiana: Demerara-Essequibo R. R., July 15, 1922, *357*.

Study of this fungus of different ages shows that the hypostroma first develops quite extensively in the palisade and mesophyll, then breaks through the cuticle and grows outward forming a thin, flat, smooth, approximately circular disk of truly radiate, i. e. Microthyriaceous character. The edge of the subicular disk is quite unevenly erose (Figure 10)

[2] Ann. Myc., 13:272. l. c.

but central parts are regularly radiate. At first this disk is devoid of perithecia but they soon develop, one or two, later more as the subicle enlarges. Thus old colonies by both coalescence and enlargement may have well over a hundred perithecia and measure nearly a centimeter in diameter. As the perithecia develop the subicle under them thickens to true stromatic character, 80 to 150μ thick. (Figure 14) In large colonies the radiate subicle enlarges to present a margin about a millimeter wide around the colony. In certain old colonies the radiate subicle is not in evidence due to the fact that it flakes off. The central foot is 80 to 90μ thick and 150μ long and is composed of cells of different shape, arrangement and staining reaction than that of the other cells of the stroma i. e. they are arranged parallel, lengthwise of the axis of the foot, and under Pianese stain are red, while the other stroma cells are irregularly arranged or preponderantly at right angles to the axis of the foot and do not stain as above stated (Figures 7, 11.) The wall surrounding the locules is black,about 36μ thick and is lined by a hyaline layer also about 36μ thick from which, in the basal portion, the asci arise (Figure 12). Frequently a large stroma is found attached to the hypostroma by several feet (Figure 14). Such may be regarded as composites of several individuals each with a central foot, rather than as one individual with many places of attachment.

The locules, stroma, foot, and hypostroma are typically Dothideaceous in character; the flat radiate subicle is typically Microthyriaceous. Disregarding the radiate subicle the fungus falls readily within the Dothideaceae and the centrally fastened stroma places it as typically of the Coccoideae and in rather close agreement with the genus Microcyclus.

Taking cognizance of the radiate, subicle, and attempting to place the fungus in the Microthyriaceae, it shows nearest relationship to the Polystomelleae with no genus of which does it agree. In the Meliolineae one is reminded of Actinodothis by the radiation and by the stromata but our fungus differs much from this genus in spores and mycelium.

The fungus thus shows kinship with the three groups and appears to be most closely related to the Dothideaceae in which family I place it. It evidently represents a transition form between the Microthyriaceae and the Dothids. The course of evolution appears to me probably to have been somewhat as follows: A primitive Microthyriaceous fungus with haustoria reaching into the epidermis developed an extensive hypostroma connected with the superficial mycelium at one central point. The habit of forming a radiating disk around the point of central fastening then appeared. So far in its history the fungus was Microthyriaceous. Now begins the evolution of the stroma by thickening of the central region of the radiate disk and the fungus becomes Dothideaceous. As the stroma-habit developed the radiate habit of the Microthyriaceae appears to have regressed as is evidenced by the irregularity of the radiation in the present form and by the

very slight development of the radiate subicle in proportion to the size of the colony. Perhaps its entire suppression resulted in some instances.

LEVEILLELLEAE

LEVEILLINOPSIS Stevens n. gen.

Stromata prosenchymatous, of parallel hyphae, superficial from a hypostroma within the mesophyll, attached by the whole basal portion. Spores 1-celled hyaline.

4 LEVEILLINOPSIS PALMICOLA Stevens n. sp.

[Figures 15, 16)

Stromata usually located in rows on the major or minor veins, amphigenous, adjacent region of the leaf diseased or dead. Spots often 1 to 2 cm. wide, 10 to 15cm. long and of ashen color. Stromata about 1 mm. high and wide, irregularly shaped. Hypostroma of but slightly greater extent than the stromata, filling the epidermis, palisade cells and much of the mesophyll. Loculi few, large, 234 to 312 x 187 to 234μ. Asci 8-spored, 56 to 74 x 10 to 14μ, biserate. Spores elliptical, hyaline, obtuse, 14 x 17 μ, nonseptate, paraphyses filamentous, equal to length of asci or half again as long.

Of unknown species of palm.

British Guiana: Kartabo, July 24, 1922, *674.*

This fungus is strictly Dothideaceous in character and clearly belongs to the Leveillelleae as given by Theissen and Sydow. A new genus is established for it since no genus of that group is given with 1-celled spores. The hypostroma is distinctly disease producing and large areas of the involved tissue are killed.

DOTHIDEAE

BAGNISIOPSIS Theiss. and Syd.

Ann. Myc., 13:291, 1915.

5. BAGNISIOPSIS PERIBEBUYENSIS (Speg.) Theiss and Syd.

Phyllachora peribebuyensis Speg., F. Guar.
Phyllachora gibbosa Winter, Revue Myc., 7:207, 1885;
Phyllachora sellowii P. Henn. Engl. bot. Jahrb., 17:525, 1883;
Phyllachora peribebuyensis Speg. var. *bullosa* Rehm: Hedw., 36: 358, 1897.

On unknown plant of the Melastomataceae.

British Guiana: Tumatumari, July 12, 1922, *223, 972.*

This fungus appears, from the numerous collections and many references in literature, to be very widespread. In Stevens' Porto Rican collections it is represented by many numbers.[3] Notwithstanding these facts

[3] Garman, P. Some Porto Rican Parasitic Fungi. Myc., 7:337, 1915.

ascigerous material is found only once in Stevens' Trinidad or Guiana material, specimen No. 972. Specimen No. 223 has the general appearance of Bagnisiopsis peribebuyensis and in section the structure of the stroma agrees with that species. No asci, however, are found in any of the stromata, but instead, numerous cavities bearing filiform conidia are found. Similar conidia are in specimen No. 972. Search through literature has failed to reveal to us any evidences of previous mention of a conidial stage of this fungus. The presence of asci in the same stromata with the conidia is sufficient to establish the identity of this conidial form with *Bagnisiopsis peribebuyensis* and we therefore describe the conidial stage of it as follows:

Stroma as described for *B. peribebuyensis*.[4] Conidial locules 0.05 to 0.15 mm. in diameter. Conidia colorless, crooked, filiform, 21 to 29 x 1 to 1.5μ.[5]

AMERODOTHIS Theiss. and Syd.

Ann. Myc., 13; 295, 1915.

6. AMERODOTHIS GUIANENSIS Stevens n. sp.

[Figures 17 to 19, 90.]

Spot irregular, pale, mycelium within the veins and producing loose stromata within the cortex which later become erumpent, superficial portion brown to black and of Dothideoid character. Stromata on the veins solitary or scattered, amphigenous, black, bearing few to several locules. Locules, ostiolate, papillate, 90 to 170μ in diameter. Asci 61 to 94 x 7μ, clavate, aparaphysate, spores 21 to 65 x 2μ, hyaline, filiform, continous, straight or slightly crooked, with a small knob at each end.

On unknown legume.

British Guiana: Rockstone, July 16, 1922, *424*.

The spot is very variable in size and shape consisting of pale to yellow regions between the affected veins, often 2 cm. or more in extent. Recently affected veins are without stromata but are slightly discolored due to the mycelium within, and the adjacent parts of the lamina are pale and sickly. In older portions the stromata are crowded, in younger parts they occur singly. While the erumpent stromata are often clearly Dothideoid, i. e. of palisade cell arrangement and erumpent, this character is not so pronounced as is often the case, indeed at times the cell arrangement is quite irregular. Still it appears to me that the fungus should be placed in the Dothideae where it comes nearest to Amerodothis in which genus I place it. Four species are given by Theissen and Sydow all of which are very different from mine in spore dimensions and shape and especially do they disagree with the spores of my species as regards the knobbed ends. Each locule is surrounded by a definite wall and in young

[4] Ann. Myc., 13:292, 1915.

[5] Notes and description by Stevens and Manter.

specimens the stroma is but little developed; the fungus then appears to belong in the Sphaeriaceae. No genus in the Sphaeriaceae presents characters showing affinity with it. The grouping of the stromata near the veins is very characteristic, (Figures 17, 90). Most of them are immediately on the veins, others are in the leaf tissue near the vein. They may be located deep within the tissue or may originate merely subepidermally.

ULEODOTHIS Theiss. and Syd.

Ann. Myc., 13:305, 1915.

7. ULEODOTHIS PASPALI Stevens n. sp.

[Figures 20 to 23.]

Stromata occupying the whole region between the upper and lower epidermis, eventually erumpent, pseudo-parenchymatic. No clypeus on either surface. Perithecia 1 to 30 in a group on a single stroma, epiphyllous. Locules small, 62 to 108μ in diameter, round or somewhat flattened, ostiolate, often somewhat rostrate. Asci numerous, 8-spored, linear, 60 to 72 x 7μ, inordinate. Paraphyses filiform, equalling the asci in length. Spores 14 to 18 x 3.5μ, fusiform, 1-septate, hyaline, guttulate.

On *Paspalum conjugatum.*

British Guiana: Coverden, August 8, 1922, *759.*

The stromata are very characteristic, separating this from Phyllachora on the stroma character alone, consisting of compact masses of smoky pseudoparenchyma filling the space between the two leaf surfaces. (Figure 20.) On the upper surfaces of these, but subepidermal, develop the locular portions, eventually becoming erumpent and usually very numerous on each stroma. The absence of a clypeus is also distinctive. While the locules sometimes have a lining consisting of one or two rows of cells darker than the remainder of the stroma such a lining is not always present and I regard the fungus in the summation of its characters as Dothideaceous rather than Sphaeriaceous. It does not agree with any of the three species, all South American, given by Theissen and Sydow.

ACHORELLA Theiss. and Syd.

Ann. Myc., 13:340, 1915.

8. ACHORELLA GUIANENSIS Stevens n. sp.

[Figures 24 to 27, 91, 92.]

Stromata scattered over the leaf, numerous, amphigenous. Perithecia spherical, in clusters usually from 3 to 8, black, slightly rough. Locules spherical, 185 to 215μ in diameter with no differentiated perithecial wall. Asci 8-spored, inordinate, 65 to 72 x 14 to 18μ. Paraphyses numerous, hyaline, filiform, gelatinous, crooked. Spores oblong, 22 to 29 x 5 to 7μ, septate, brown, constricted at the septum.

On *Mikania* sp. (?)

British Guiana: Coverden, August 8, 1922, *763* (type); Wismar, July 14, 1922, *294*; Rockstone, July 16, 1922, *438;* Kartabo, July 22, 1922, *563.*

The general characters of this fungus are Dothideaceous and it agrees well with Achorella. The hypostroma is Dothideaceous in character and often the stroma is so too, the perithecia touching each other and fusing (Figure 24), thus the locules with undifferentiated walls appear in a stroma. In other instances spherical perithecia develop upon the stroma, only partically or not at all attached to their neighbors. In such cases the fungus appears to be Sphaeriaceous rather than Dothideaceous and it clearly represents a border-line form between two groups.

PHYLLACHORACEAE

SCIRRHIINEAE

Anisochora Theiss. and Syd.

Ann. Myc., 13:406, 1915.

9. Anisochora tabebuiae Stevens n. sp.

[Figures 28 to 31, 94.]

Spot large, 7 cm. or more, portion between veins pale yellow to brown. Stromata on the veins, strongly developed epiphyllous, very slightly hypophyllous, black, 0.7 to 2 mm. wide, of indeterminate length, frequently 7 cm. or more, rarely spreading over the leaf surface as a flat crust. Stromata developing as a thick (about 200 to 450μ) cushion of vertical, parallel (palisade-like) hyphae between the epidermis and the palisade tissue, covered by a black, epidermal clypeus. Phloem browned, due to mycelial invasion. Locules few, 1 to 4 in cross section of a stroma, subglobose, 275 to 460μ broad, about 310μ deep, ostiolate. Asci 8-spored, uniseriate or inordinate, 90 x 10 to 11μ. Spores 11 to 13 x 5.5 to 7μ, hyaline, unequally 1-septate, lower cell very small. Paraphyses few.

On *Tabebuia* sp.

Trinidad: St. Augustine, August 13, 1922, *847.*

The stromata upon the veins form a very distinctive feature (Figure 94) and from their nature indicate the migration of the fungus through the veins which is also substantiated by the evidence of phloem infection found in cross sections. In some instances there are breaks, sometimes a centimeter long, in a stroma, though there are evidences in the color of the vein that it is diseased in the non-stromatic portion. The palisade stroma is nearly colorless and consists of very thin walled cells of remarkable thickness (about 18μ), (Figures 28 to 30). On the hypophyllous side of a vein there is a slight development of palisade stroma similar to that on the upper

side, but much less extensive and with but scant clypeus. Irregular locules occasionally develop bearing no asci, but numerous filamentous bodies, Septoria-like, which appear to be conidia. Only one species of Anisochora is given by Theissen and Sydow and that on Ficus. My species differs essentially from that and is on a very different host family.

SCOLECODOTHOPSIS Stevens n. gen.

Stromata in the leaf mesophyll, without clypeus, not prosenchymatic. Perithecia dothideaceous, isolated, deeply immersed and remaining so, opening by an ostiole to the surface. Ascospores filiform.

10. SCOLECODOTHOPSIS INGAE Stevens n. sp.

[Figures 32 to 34, 95.]

Spots large 1 to 3 cm. in diameter, roughly circular, yellow or tan-colored, border indefinite, shading into the normal leaf; occupied by numerous black regions, 1 to 2 mm. in diameter, appearing black from both sides of the leaf. Stromata in the mesophyll, dense, hyaline. Locules 1 to several in each stroma, about 300μ broad and 100μ deep. Ostiole protruding by a slight, dark papilla, often lateral or oblique. Asci 8-spored, 94 x 10μ. Spores long, filiform, 18 to 60 x 3μ, straight or slightly curved, often slightly thicker near the middle, several-septate.

On *Inga* sp.

British Guiana: Demerara-Essequibo R. R., July 15, 1922, *406* (type); Tumatumari, July 8, 1922, *58;* Kartabo, July 21, 1922, *510.*

The contents of the cells of the upper epidermis in the region of the stromata are blackened and similar blackening appears between the palisade cells, though without any extensive development of mycelium in this region. On the lower surface however the epidermis and adjacent region are packed with a dense mycelial development. The taxonomic position of this fungus is uncertain. The large stromatic development in the mesophyll with the separate locules appear to warrant its inclusion in the Dothideales and the absence of a clypeus and of a palisade hyphal arrangement would place it here in the Eu-Montagnelleae of Theissen and Sydow. This group is on the boundary line between the Dothids and the Sphaeriaceae and distinction between these groups is difficult.

In the Eu-Montagnelleae the only genus given with filamentous spores in Ophiocarpella. Indeed filamentous spores either in the Dothids or in the Sphaeriales are rare. Comparison with the specimens of *O. tarda*,[6] as well as with the description, show the fungus to be generically quite different. Taking into consideration all of the characters, the fungus appears to me to be best placed in the Eu-Montagnelleae as a new genus.

[6] Ellis and Everhart, North American Fungi, no. 1585.

PHYLLACHORINEAE

PHYLLACHORA Nits.

In Fuckel Symb. Myc., 216, 1869.

11. PHYLLACHORA AEGIPHILAE Stevens, n. sp.

[Figure 35.]

Spots minute, 1 to 2 mm., consisting of a pale halo around the usually solitary stroma. Stromata punctiform, rough and black above; appearing only as raised places below, less than 1 mm. in diameter. Clypeus epiphyllous, epidermal. Stroma occupying the whole of the mesophyll with a dense pseudo-parenchyma. Locules few, usually 1 to 4, 180 to 216μ in diameter by 180μ deep. Asci 8-spored, 14 x 7.5μ; paraphyses filiform; spores fusiform, hyaline, continuous, 17 to 25 x 4.5 to 5.5μ.

On *Aegiphila* sp.

British Guiana: Rockstone, July 17, 1922, *458*.

Five species of Phyllachora are given by Theissen and Sydow as on members of the Verbenaceae but all disagree essentially with the one described above. The characteristic features are the epiphyllous, epidermal clypeus and the absence of a hypophyllous one. The ostiole develops through the clypeus i.e. on the upper surface.

12. PHYLLACHORA CHAETOCHLOAE Stevens n. sp.

[Figures 36 to 38, 97.]

Stromata black, shining, conspicuous from above, rarely visible below. Arranged in longitudinal groups from 3 to 12 cm. long. Single stromata small, punctiform but by coalesence often 1 x 10 mm. in size. Locules numerous, globular (about 125μ in diameter) or flattened (310μ in diameter, 110μ thick), ostiolate, occupying the palisade region and upper portion of the mesophyll. Clypeus on the upper surface thick (45 to 60μ), epidermal. Asci 108 x 14μ, spores inordinate, oblong, continuous, hyaline, 7 x 14 to 18μ. Conidia are very commonly produced in young portions of the ascigerous stroma, in ostiolate, clypeate, locules like those bearing asci. Conidia cylinderical, hyaline, obtuse, straight or slightly crooked, guttulate, continuous or 1-septate, 12.5 to 23 x 2 to 3.6μ Filiform conidia produced as are the cylindrical. Conidia 22 to 29 x 1μ, hyaline, usually flexuose, sometimes straight, usually slightly larger at one end than at the other.

On *Chaetochloa tenax*.[7]

Trinidad: Cumuto, August 15, 1922, *882*.

No Phyllachora is given as on Chaetochloa by Theissen and Sydow; two are given as on Setaria both of which agree reasonably well in spore shape and size with our species, but disagree essentially with them in stroma characters and conidial forms.

[7] Determined by Mrs. Agnes Chase.

13. PHYLLACHORA CONGRUENS Rehm.

Leaflets Phillip, Bot., 6:2220, 1914.

On *Valota laxa*.

Trinidad: Cumuto, August 16, 1922, *894*.

14. PHYLLACHORA DIMORPHANDRAE Stevens n. sp.

[Figures 39 to 41, 96]

Stromata black, shining above, dull below, very irregular in shape, 2 to 15 mm. across, arched above, the whole mesophyll occupied by a loose stroma; clypeus on each surface. Clypeus 18 to 36 μ thick, epidermal and subepidermal. Locules 30 per stroma, in one row, when young near the upper leaf surface, but developing to fill the leaf space and opening hypophyllous; very large and irregular, 390 to 520 x 179 to 310μ. Asci 8-spored, 115 x 7μ, long-stalked. Paraphyses filamentous, gelatinous. Spores uniseriate, hyaline, continuous, oblong, obtuse, 7 to 11 x 5μ.

On *Dimorphandra* sp.

British Guiana: Wismar, July 14, 1922, *291;* Demerara-Essequibo R. R., July 15, 1922, *333* (type); Kartabo, July 22, 1922, *629*.

More than fifty species of Phyllachora are listed by Theissen and Sydow on the Leguminosae but all of these differ from this species in one or more essential characters.

The mycelium between the two clypei is very fine, hyaline and loosely pervades the whole mesophyll region, somewhat darkening the host cells. Each locule is lined by a layer of mycelium about 10μ thick thus constituting a very thin but no less actual perithecial wall (Figure 40). Notwithstanding this the fungus is truly Dothideaceous in summation of characters. The origin of the locules close to the upper part of the leaf seems constant. As they enlarge they soon come to press against the epiphyllous clypeus and as they mature they develop a beak-like protuberance which presses through the mesophyll to the lower clypeus; breaks through this and becomes osteolar.

15. PHYLLACHORA ENGLERI Speg.

Guaranit. I. No. 267 On *Anthurium* sp.

British Guiana: Coverden, August 5, 1922.

This remarkably beautiful specimen agrees closely with the published descriptions.

16. PHYLLACHORA GUIANENSIS Stevens n. sp.

Stromata oval, small, about 1 mm. long, scattered, black, shining, surrounded by a zone of dead brown tissue forming an oval spot 2 to 4 mm. in size. Much more commonly conspicuous above than below. Loculi globular, few in each stroma, usually not more than six, located strictly in

the mesophyll, 125 to 170μ in diameter. Clypeus on both leaf surfaces but much more extensive above, about 18μ thick. Stroma of the mesophyll region of a loose network of mycelium. Asci cylindrical with filiform paraphyses. Spores uniseriate, hyaline, continuous, elliptical, 11 x 3.6μ.

On *Paspalum virgatum*.

British Guiana: Tumatumari, July 9, 1922, *32*; July 10, 1922, *142:* Georgetown, Lamada canal, August 2, 1922, *712:* Coverden, August 4, 1922, *730*.

This Phyllachora is distinguished from *P. paspalicola* both by its thin spore and by the character of its spot.

17. Phyllachora paspalicola P. Henn.

Hedw., 48:106, 1908.

On *Paspalum arenarum*.

British Guiana: Rockstone, July 16, 1922, *430*.

On *Paspalum conjugatum*.

British Guiana: Rockstone, July 16, 1922, *419*.

The stromata in specimen No. 419 are chiefly on the laminae.

Four species of Phyllachora are given by Theissen and Sydow as occuring on Paspalum viz, *P. acuminata* Starb., *P. infuscans* Wint., *P. paspalicola* P. Henn. and *P. winkleri* Syd. All but the last of these were collected in South America.

Specimen No. 430 agrees closely with *P. paspalicola* and differs markedly from each of the others. The stromata occur chiefly on the leaf sheaths, not on the blades.

18. Phyllachora phaseoli (P. Henn.) Theiss. and Syd.

Ann. Myc., 13:507, 1915.

Physalospora phaseoli P. Henn. Hedw., 43:368, 1904.

Physalospora atroinquinans Rehm Hedw., 44:5, 1904.

Hyponectria phaseoli Stev. Bot. Gaz., 70:401, 1920.

On unknown Legume.

British Guiana: Kartabo, July 21, 1922, *517*.

19. Phyllachora tabernaemontanae Stevens n. sp.

[Figures, 42, 43, 98.]

Stromata dull black, equally visable above and below, irregular in outline, large, 4 to 10mm., bearing numerous locules apparent externally from both above and below as small mounds, occupying the mesophyll with a loose, black, net work covered above and below by clypei which extend slightly beyond the stroma of the mesophyll. Locules flat, broad, 290 to 340μ, 90 to 110μ deep; wall about 70 to 80μ thick, black. Asci 8-spored, 90

to 97 x 18μ; spores inordinate. Paraphyses numerous, filiform, gelatinous. Spores continuous, hyaline, 11.14 x 7μ, elliptical, obtuse.

On *Tabernaemontana* sp.

British Guiana: Kartabo, July 22, 1922, *564*.

20. Phyllachora tiliae Stevens n. sp.

[Figures 44 to 46.]

Spot irregularly circular, 2 to 10 mm. in diameter, tan-colored, bearing numerous, usually 10 to 20, stromata, Stromata epiphyllous, punctiform, circular, black, shining, 1mm. in diameter, often coalescing, usually with a minute central papilla. Appearing below merely as swollen spots. Stromata usually unilocular, in the mesophyll, with thick clypeus above and below. Asci 8-spored, 70 to 83 x 7 to 10 μ. Paraphyses numerous, gelatinous. Spores 11 to 14 x 4μ, hyaline, continuous, oblong.

On unknown species of the Tiliaceae.

British Guiana: Tumatumari, July 12, 1922, *227*.

This differs from *P. paraguaza* Speg. in having more narrow spores: from *P. clypeata* Theiss. in the character of the clypeus; from *P. grewiae* in both spores and clypeus.

21. Phyllachora ulei Wint.

Grev., 15:90, 1886.

On *Dioscorea* sp.

British Guiana: Coverden, August 5, 1922, *746*, and August 8, 1922, *801:* Rockstone, July 17, 1922, *545*.

The last number is on a species of Dioscora different from that of the others and the locules are larger and fewer in number.

22. Phyllachora wismarensis Stevens, n. sp.

[Figures 47 to 50, 99.]

Stromata 1 to 3 mm. in diameter, circular or irregular, black, dull, raised, chiefly hypophyllous but occasionally showing from both sides of the leaf, locules usually 1 to 6 showing externally as slightly raised points; occupying the mesophyll and epidermis. Locules 300μ or more in diameter. Asci 126 to 170 x 11 to 14μ. Spores 32 to 36 x 7 to 8μ, hyaline, continuous, larger at one end, obtuse, tapering toward small end. Paraphyses numerous, filiform. Conidia filiform, continuous, hyaline, curved, 14 to 23 x 1μ, occurring singly on conidiophores within the locules.

On *Ficus* sp.

British Guiana: Demerara-Essequibo R. R., July 15, 1922, *397* (type) and *334*.

Eight species of Phyllachora are recorded on Ficus by Theissen and Sydow. From *P. catervaria* (Berk.) Sacc. ours differs in size and location of stromata also essentially in shape and size of spores; from *P. pseudes* Rehm. in shape and size of spores; from *P. effigurata* Syd., a Brazilian

species, in the arrangement of the stromata and shape and size of spores; from *P. vinosa* Speg. from Brazil, in shape and size of spores; from *P. ficicola* All. and Henn. also Brazilian, in stroma characters and in spore shape and size; from *P. aspideoides* Sacc. and Berl. from Brazil, in stroma and spore size and shape; from *P. amaniensis* P. Henn. in spore size and shape; from *P. devriesei* Koord in stroma and spore size and shape.

The stromata are scattered over the leaf but are more common near veins though not on veins. The stromatic development is large resulting in much thickening in the occupied part such that a leaf normally 230μ thick is often 700μ. (Figure 47) The clypeus covering the loculi is often 80μ thick.

The conidial stage falls in the Sphaerioidaceae-Scolecosporae. Spores borne in the stromatic locules, and apparently singly on the conidiophores would bring it close to Septosporiella. However, spores of Septosporiella are colored.

The following six Phyllachoras are given by number only, with descriptions, because the host is unknown. It is quite probable that all are new species but in the absence of knowledge as to the identity of the host it is thought best to publish them thus without names.

23. Phyllachora No. 1.

[Figure 51.]

Spot 3 to 8 mm. in diameter, yellow. Stromata 1 to 2 mm. in diameter, black from both leaf surfaces, surrounded by a pale zone about 3mm. wide, with a clypeus above and below. Locules 90 to 320μ wide, 90 to 180μ deep, ostiolate, uniseriate, Asci 8-spored, 90 x 7 to 9μ. Paraphyses filiform, hyaline. Spores hyaline, continuous, 11 x 7μ, oblong, obtuse.

On unknown host.

British Guiana: Tumatumari, July 10, 1922, *149:* July 9, 1922, *41.*

The host is possibly Anonaceous, if so the species is new.

24. Phyllachora No. 2.

[Figures 52 to 54, 100, 102.]

Stromata epiphyllous, very numerous, punctiform, black, about 1mm. in diameter, uniloculate, rarely biloculate, scattered evenly over large areas, in the epidermis and palisade region and extending about half way into the mesophyll. Clypeus epiphyllous. Locules 185 to 380μ wide, ostiolate. Paraphyses filamentous, gelatinous, crooked. Asci 8-spored, 88 x 11 to 14μ, spores inordinate. Spores continuous, hyaline, oblong, obtuse, 7 to 9 x 12 to 18μ. Pycnidial cavities similar to the perithecial; conidia filiform on linear conidiophores.

On unknown host.

British Guiana: Tumatumari, July 9, 1922, *89.*

25. Phyllachora No. 3.

Spot none, stromata small, punctiform, 1 to 1.5μ in diameter, black, shining, visible from both sides of the leaf, both surfaces arched, with few locules, usually 1 to 4. Clypei on both surfaces very thick and black, epidermal and sub-epidermal. Locules 230 to 277μ in diameter or by coalescence 550μ. Asci 8-spored, long, narrow, 80 x 5.5μ, paraphyses hyaline, filiform, crooked, gelatinous; spores uniseriate or inordinate, 11 to 12.5 x 4 to 5μ, continuous, hyaline, oblong.

On unknown dicotyledonous host.

British Guiana: Coverden, August 4, 1922, *981.*

Associated with Kusanoopsis Stevens and Weedon.[8]

26. Phyllachora No. 4.

[Figure 101.]

Spot pale, circular, constituting a zone 1 to 2 mm. wide around each stroma. Stromata punctiform, about 1 to 3 mm. in diameter, black, visible from both sides of the leaf, uniloculate. Clypeus epidermal, 30 to 46μ thick on both leaf surfaces. Locules about 300μ wide, 154 to 185μ deep. Asci long, narrow, 68 to 7μ. Paraphyses filiform, few. Spores uniseriate, hyaline, continuous, ovate, 9 to 11 x 7μ.

On unknown dicotyledonous plant.

British Guiana: Wismar, July 14, 1922, *276.:* Kartabo, July 23, 1922, *618.*

27. Phyllachora No. 5.

[Figure 55.]

Spot small, 5 to 8 mm., yellowish. Stromata scattered, visible from both sides of the leaf, usually unilocular, rarely bilocular, clypeus above and below and frequently extending into the mesophyll to surround the locule; about 30μ thick, dense, black. Locules globular, 180 x 108μ. Asci 8-spored, long, narrow. Paraphyses filiform, numerous. Spores continuous hyaline, oval to elliptical, 11 x 7 to 8μ.

On unknown Legume.

British Guiana: Coverden, August 8, 1922, *780:* Tumatumari, July 8, 1922, *47:* and July 10, 1922, *138.*

The clypeus develops first in the upper and lower epidermis, black and dense, then often extends into the mesophyll completely surrounding the locule by a black stroma quite like the clypeus, both in thickness and character, (Figure 55).

The fungus is clearly a Phyllachora and the only feature of special interest is the manner in which the locule is enveloped.

[8] Stevens, F. L. and Weedon, A. G. Three new microthyriaceaus fungi from South America. Mycologia, 15:197, 1923.

28. Phyllachora No. 6.

[Figure 103.]

Spot pale yellow extending in a 2 to 3 mm. zone around the stromata. Stromata dull black, visible from both surfaces, 1 to 2 mm. in diameter, flat. Stromata occupying the whole of the mesophyll. Upper and lower clypeus epidermal, extending somewhat beyond the stroma of the mesophyll. Locules few, small, 150μ in diameter, each with a lining wall about 15μ thick, of character quite distinct from that of the stroma. Asci 8-spored, 60 to 65 x 7 to 11μ. Paraphyses filiform. Spores oval, hyaline, obtuse, 18 x 5μ, inordinate.

On unknown host.

British Guiana: Tumatumari, July 10, 1922, *139*.

Endodothella Theiss. and Syd.

Ann. Myc., 13:582, 1915.

29. Endodothella anacardiacearum Stevens n. sp.

[Figure 56.]

Stromata scattered between the veins, 1 to 2 mm. in diameter, black below, brown above, causing hypertrophy of the leaf, doubling its thickness, consisting of a rather close pseudoparenchyma occupying the mesophyll throughout its thickness and with thin clypei above and below extending slightly beyond the stroma. Locules many, irregularly placed, subglobose, 50 to 215μ broad, 140 to 300μ deep. Asci 8-spored, 83 to 90 x 7μ. Paraphyses filiform, crooked, gelatinous. Spores 1-septate, 11 to 14 x 3.6μ.

On unknown species of the Anacardiaceae.

British Guiana: Demerara-Essequibo R. R., July 15, 1922, *353:* Tumatumari, July 8, 1922, *973*.

The stromata develop very irregularly, deforming all tissues and producing the greatest hypertrophy below. (Figure 56).

30. Endodothella tapirae Stevens n. sp.

[Figures 57 to 59]

Stromata scattered, circular, about 1 mm. in diameter, showing black from one or both leaf surfaces; surrounded by a pale zone about 1 mm. in width. Stromata often raised to double the thickness of the leaf; located in the mesophyll, consisting of a rather compact, black, pseudoparenchyma with clypei on one or both surfaces; paraphyses many, filiform. Asci long, narrow, 83 x 7μ, 8-spored. Spores 11 x 3.5μ, ovate, 2-celled.

On *Tapira* sp.

British Guiana: Kartabo, July 22, 1922, *525*. Specimen in packet filed under *Myriangenella tapirae* Stevens & Weedon.

The fungus is a typical Phyllachora except that the spores are two-celled. The stromata are quite uniform in size and in all sections studied showed either three locules on one side of a leaf, (Figure 57) or 3 on each

side (Figure 58). The spot surrounding the stroma is also uniform and since no mycelium could be found outside of the stroma it is probably due to chemical rather than mycelial invasion. The specimens bear also a Myrianginella.

MONTAGNELLACEAE

EU-MONTAGNELLEAE

HAPLOTHECIUM Theiss. and Syd.

Ann. Myc., 13:614, 1915.

31. HAPLOTHECIUM GUIANENSE Stevens n. sp.

[Figures 60 to 62, 104.]

Stromata 1 to 2 mm. in diameter showing from above and below, black, subcircular, surrounded by a very narrow (0.5 mm.) brown line, this by a zone 1 to 2 mm. wide that is pink to rose which gradually shades off into healthy tissue. Stroma occupying the whole mesophyll, consisting of a very loosely woven mycelial network with a black clypeus in both upper and lower epidermis. Locules globular to pyriform, ostiolate, in two rows opening through the upper and lower epidermis, 170 to 260μ. in diameter. Asci 8-spored, 100 x 18μ, uniseriate or inordinate. Paraphyses filiform, gelatinous. Spores oval, 12 x 7μ, hyaline, continuous.

On unknown lactiferous dicotyledonous leaf (Simarubaceae?).

British Guiana: Demerara-Essequibo R. R., July 15, 1922, *376*.

The stroma in the mesophyll consists only of a very loose hyphal network mainly occupying the intercellular spaces. In the palisade region the mycelium presses between the cells and kills them but no compact stroma develops. The epidermal cells, however, are compactly filled with mycelium thus forming a clypeus.

The loose hyphal character of the stroma clearly shows relationship to the Montagnelleae in which the fungus would fall in the section Eumontagnellaceae and in the genus Haplothecium Th. and Syd. where it would certainly be placed were it not for the presence of an epidermal clypeus. This clypeus would indicate that it should be placed in the Phyllachoraceae where it could only fall in the genus Phyllachora. Since the fungus all in all agrees more closely with Haplothecium than Phyllachora I place it as above indicated.

HEMISPHAERIACEAE

Gymnopeltineae Stevens and Guba mss.[9]

GYMNOPELTIS Stevens n. gen.

Ascoma like the Thrausmatopeltineae but red and with asci solitary, scattered: spores unequally 2-celled, hyaline.

[9] Publications of the Bishop Museum, *in press*.

32. Gymnopeltis trinidadensis Stevens n. sp.

[Figures 63 to 65.]

No free mycelium. Ascomata superficial, scattered, punctiform, red, 380 to 460μ in diameter, thin, flat. Asci solitary, scattered, naked, subglobular, 8-spored, 22 to 25 x 18μ, stipitate. Spores hyaline, unequally 2-celled, 11 x 3.5μ, large at one end tapering to the other end, obtuse.

On *Mauritia*.

Trinidad: Cumuto, August 16, 1922, *979*.

This fungus in its flat, non-radiate ascoma shows closest kin-ship to the Thrausmatopeltineae from which it is separated by the scattered, naked asci, a combination of characters that led Stevens and Guba to erect the group Gymnopeltineae to which the present fungus clearly belongs, though it differs in many ways from the genus, Hexagonella, the only other known member.

PERISPORIACEAE

Key to genera involved.

Perithecium and mycelium superficial, mycelium without hyphopodia.
- Setae present.
  - Perithecial setae simple
    - Spores hyaline ..... Dimeriella p. 26
    - Spores brown.....
      - 2-celled.....
        - Aparaphysate..... Phaeodimeriella p. 27
        - Paraphysate..... Meliolinopsis p. 27
      - 4 to 6-celled..... Hyalomeliolina p. 27
  - Perithecial setae forked..... Oplothecium p. 28
- Setae absent or atypical
  - Perithecium setose ..... Haraea p. 29
  - Perithecium smooth, spores brown, 2-celled
    - Perithecium red..... Parodiopsis p. 29
    - Perithecium black..... Dimerium p. 31
    - Perithecium yellow..... Mycophaga p. 31
- Perisporiaceae imperfecti..... Pycnodothis p. 32

Dimeriella Speg.

Fung. aliquot Paulistani p. 12 in Revista del Museo de La Plata 15: 1908.

33. Dimeriella erigeronicola Stevens.

Ill. Acad. Science 10:166 to 167, 1917.

On *Erigeren bonariensis*.

British Guiana: Tumatumari, July 11, 1922, *204*.

This fungus agrees with *Dimeriella erigeronicola* found by Stevens in Porto Rico.

33a. Dimeriella cordiae (P. Henn.) Theiss.

Zur Revision der Gattung Dimerosporium, in Bot. Cent. Beihefte 29:67. 1912.

Dimerosporium cordiae P. Henn. Fungi. S. Paulenses IV. in Hedw., 48:4,1908.

On *Cordia* sp.

Trinidad; Port of Spain, Aug. 14, 1922, *863:* St. Augustine, Aug. 13, 1922, *824:* St. Clair, Aug. 15, 1922, *892.*

Phaeodimeriella Speg.

Fungi aliquot Paulistani.

34. Phaeodimeriella asterinarum (Speg.) Theiss.

Dimerosporium asterinarum Speg. F. Puigg., n. 216.

On unknown species of the Microthyriaceae, on unknown member of the Anonaceae.

British Guiana: Rockstone, July 16, 1922, *421.*

Meliolinopsis Stevens n. gen.

Perisporiaceous, like Meliolina except that the spores are 1-septate.

35. Meliolinopsis palmicola Stevens n. sp.

[Figures. 66, 67.]

Mycelium amphigenous, superficial, aggregated in dense clumps around the perithecia and spreading in a loose network over the surrounding leaf surface; black in mass; single strands pale yellow by transmitted light, slightly crooked, non-hypophodiate. Perithecia in groups in the centers of the colonies, smooth, globose, non-ostiolate, about 275μ in diameter. Setae simple, black, crooked, almost uncinate, obtuse, very numerous around the perithecium, thicker and darker than the mycelium, 200 to 300μ long, 4μ thick. Asci not evanescent, usually 4-spored, surrounded by very numerous gelatinous, hyaline, filiform paraphyses which are crooked and longer than the asci. Spores dark brown, 2-celled, obtuse, strongly constricted, surrounded by a thin hyaline, gelatinous sheath, 40 to 65 x 20 to 25μ.

On *Baetris* sp.

Trinidad: Cumuto, August 16, 1922, *1000.*

This species agrees with Meliolina except for its 1-septate spores and for the very numerous gelatinous paraphyses. The spores in shape strongly resemble those of *Meliolina guaianensis* and these two forms together constitute interesting links connecting this one-septate Meliolinopsis with the genus Meliola.

Hyalomeliolina Stevens n. gen.

Persporiaceous, perithecial setae long, simple, mycelium-like; asci persistent; spores 3 to 5-septate, brown, end cells pale to hyaline.

36. Hyalomeliolina guianensis Stevens n. sp.

[Figures 68 to 70, 105, 107.]

Colonies superficial, black, circular, 2 to 4 mm. in diameter, amphigenous but mostly hypophyllous. Mycelium black, smooth, non-hypho-podiate, uniform in diameter, 4μ, slightly crooked, very sparsely, branched. Perithecia few to many in each colony, buried in the mycelial tangle, globose, black, 180 to 216μ in diameter, slightly rough: bearing many black, simple setae, often over 1000μ long, mycelium-like. Paraphyses numerous, filiform, gelatinous. Asci persistent, 94 to 115 x 22 to 25μ, 6 to 8-spored. Spores inordinate, dark, elliptical-fusiform, 32 to 43 x 9 to 11μ, unequally 3-septate (sometimes 5-septate), strongly constricted at the central septum. Two end cells very small and much lighter in color than the others. Two-celled when young.

On *Licania* (?).

British Guiana: Rockstone, July 17, 1922, *454* (type); Kartabo, July 24, 1922, *665*.

The mycelium forms a densely wooly colony and its filaments show a tendency to twist together in a ropy fashion that is quite characteristic. (Figure 69, 106). The spores with the strong constriction at the middle and with the two end cells small and pale are quite distinctive. In general appearance the fungus shows relationship with the genus Meliolina; in the abundant, black superficial mycelium without hyphopodia, and in the possession of setae. It differs from members of that genus in that its spores are not like typical Meliola spores but have the terminal cells pale to hyaline.

Oplothecium Syd.

Ann. Myc., 21: 97, 1923.

37. Oplothecium palmae Stevens n. sp.

Fungus superficial, hypophyllous. Perithecia globular, sometimes turbinate, about 50 to 60μ in diameter. Perithecial setae 1-11 per perithecium, short, about 11μ long, ending with 3-4 spikes each about 8μ long. Asci many with numerous filiform, hyaline paraphyses, about 18 x 3.6μ, containing 16 hyaline, single-celled, ovate spores. Mycelium very fine, forming a tangled net-work.

On Palm.

British Guiana: Tumatumari, July 11, 1922, *134*.

This exceedingly interesting fungus appears to agree closely with the descriptions and figures of Sydow drawn from material collected in the Philippine Islands with the exceptions that no mycelial setae are observed on our specimens while described as copious on Sydow's specimen. The perithecial setae on our material are somewhat shorter, 11μ as against 10 to 18μ, and their branches are also shorter, 8μ as against 10 to 18μ. Sydow

states that the fungus is questionably capnodiaceous; it appears, however, to me to be perisporiaceous, and I so place it.

HARAEA Sacc and Syd.

Ann. Myc., 11:312, 1913.

38. HARAEA MAURITIAE Stevens n. sp.

[Figures 71–76]

Mycelium superficial, smooth, brown, 3.5μ thick, freely anastomosing, bearing pseudohyphopodia either axillary to the branches or laterally. Perithecia globose, densely setose, astomate, 123 to 154μ in diameter. Perithecial setae 54 to 154μ long, otuse, tapering, 7μ thick at the base, 3μ at apex. Asci 92 to 123μ, ovate, stipitate. Spores 50 to 61 x 10 to 11μ, hyaline and 1-septate when young, constricted and readily separating, cylindrical, straight or slightly curved, ends rounded, usually slightly unequally divided, 3-septate and brown when mature.

On *Mauritia* sp.

Trinidad: Guanapo, August 16, 1922, *908*.

The pseudohyphopodia are peculiar consisting of a stalk cell either short (to sessile) or long (10-25μ) and a head usually about 27x14μ consisting of a tangle of cells (Figure 76). The function of these is unknown.

PARODIOPSIS Maub.

Bul. Soc. Myc. de France, 31:3, 1915.

This genus was established on the species *Parodiella melioloides* Wint. because this species possesses an abundant superficial mycelium which properly is not found in Parodiella. The genus is regarded by Theissen and Sydow[10] (1917) as belonging to the Perisporiaceae. Arnaud[11] places the genus in his tribe Parodiopsidees in his family Parodiellinacees and unites with Parodiopsis the following genera: Chrysomyces Theiss and Syd., Schistodes Theiss., Hypoplegma Theiss and Syd. Perisporiopsis P. Henn. and Piline Theiss. Theissen and Sydow regard only one species of the genus as tenable while Arnaud recognizes five species as well established and six others tentatively so. Three of the tentative species of Arnaud have been placed by the other mycologists in other genera viz Chrysomyces, Perisporiopsis and Piline. In the following species determinations the conceptions of Arnaud as to the specific characters and limitations are followed.

39. PARODIOPSIS MELIOLOIDES (Wint.) Arn.

On *Alchornea cordata*.

British Guiana: Tumatumari, July 10, 1922, *153*; July 8, 1922, *63*.

This specimen agrees perfectly with the original description but the perithecia are not found in concentric rows as is so common on many other hosts.

[10] Theissen and Sydow l. c.

[11] Arnaud, G., Les Asterinées. T. 2. Ann. des Epiphyties, 7: 1921.

On unknown host.

British Guiana: Demerara-Essiquibo R. R., July 15, 1922, *331.*

The material of this collection is scant but generic agreement seems certain. The asci measure 126 x 43μ, spores 32 to 36 x 14 to 15μ. The spores when mature are dark. Though the spores measure somewhat less than as given in the description this collection is provisionally referred to *P. melioloides.*

40. Parodiopsis viridescens (Rehm) Arn.

Notes Myc., p. 23, 1915.

On *Banisteria ciliata.*

British Guiana: Coverden, July 8, 1922, *772.*

Two species of Parodiopsis are listed by Arnaud as on Malpighiaceae. Our specimen agrees most nearly with the above named species, which was made the type of a new genus, Hypoplegma, by Theissen and Sydow, which however is rejected by Arnaud. The type of the species is on an undetermined species of the Malpighiaceae collected in Brazil (Ule No. 1378) with spore measurements given by the author as 35 to 40 x 10 to 11μ, by Theissen and Sydow as 45-55 x 10-12μ. The spores of our specimen measure 32 to 36 x 11μ.

41. Parodiopsis ingarum (P. Henn.) Arn.

Les Asterinees Ann. d. l' ecole nat. d. Agr., Montpellier, 1918.

Parodiella viridescens Rehm. var. *ingarum* P. Henn.

On *Inga* sp.

British Guiana: Coverden, August 8, 1922, *782, 802.*

Our specimens agree well with the descriptions, especially so as to the color of the perithecia and the shape and size of the spores. The species of the Inga has not been determined but it is an unusual one with leaflets long and narrow, usually about 80 x 13 mm.

Arnaud mentions the presence of numerous setae resembling in their tips geniculate conidiophores though no conidia were found. My specimen shows numerous, erect hyphae also resembling geniculate conidiophores. A Heliminthosporium parasitic on the Parodiopsis is also present and is described elsewhere.

Examination of the microtome sections shows tissue to considerable depth under parts of the colonies to be heavily occupied and killed by internal mycelium.

42. Parodiopsis sp. ind.

On Apocynaceae (?).

Trinidad: Guanapo, August 16, 1922, *976.*

The specimens are clearly of Parodiopsis aspect and bear the perithecia in concentric rows but no asci could be found. Large dead spots are produced in the leaf.

DIMERIUM Sacc. and Syd.

Syll. Fung., 16:410, 190.

43. DIMERIUM GUIANENSE Stevens n. sp.

[Figures 77, 107]

Spot irregular in shape showing from both sides of the leaf, to several millimeters in diameter, dead, brown or ashen as seen from above. Superficial mycelium pale straw colored, non-hyphopodiate, non-setose, hypophyllous, abundant. Colonies yellow when young black when old. Perithecia superficial, globular, black, 105 to 185μ in diameter, smooth, surface cells agglutinated.

Asci 4-spored, clavate, hyaline, thick walled, 120 x 36μ, evanescent, several in each perithecium, imbedded in a matrix composed of tangled, gelatinous, crooked, filiform paraphyses. Spores yellow to dark brown, long pyriform to elliptical, usually tapering toward one end, 1 to 2 septate, 36 to 50 x 14 to 18μ, often truncate at one end.

On unknown rosaceous host.

British Guiana: Kartabo, July 24, 1922, *656*.

According to the key of Theissen and Sydow[12] this would fall in the genus Dimerium if the spores be regarded as 2-celled; in Perisporina if three-celled but it would be excluded from Perisporina by the absence of mycelial setae also by the presence of paraphyses. It shows many similarities with Perisporiopsis P. Henn. as figured by Arnaud[13] but differs from that genus in possessing no mycelial setae or paraphyses. Though the spores are frequently 2-septate, I place the present species in the genus Dimerium as an abberant form.

MYCOPHAGA Stevens n. gen.

Fungus superficial, perisporiaceous, non-hypopodiate, no setae on mycelium or perithecium; spores hyaline, 3-septate.

44. MYCOPHAGA GUIANENSIS Stevens n. sp.

Mycelium non-hyphopodiate, honey-yellow, forming a tangled network. Perithecia globular, non-ostiolate, 123 to 138μ, no appendages, smooth. Asci 61 to 72 x 18μ, conglobate; no paraphyses; spores 3-septate, hyaline, 32 to 40 x 3.5μ, obtuse, slightly thicker at one end and tapering gradually.

Growing as a parasite on an undetermined, hyphopodiate mycelium on Anacardium (cashew).

British Guiana: Rockstone, July 13, 1922, *253*; Tumtumari, July 8, 1922, *65*.

This fungus in general characters is close to Perisporina from which it differs in spore color, septation and in mycelium. If regarded as being

[12] Theissen and Sydow l. c.

[13] Arnaud, G. Les Asterinées. Ann. de l'Ecole nat. d'Agric. de. Montpellier. N. S. T., 16:1918.

of the Capnodiaceae it would be near Limacinia from which it differs essentially in the character of its mycelium.

PERISPORIACEAE IMPERFECTI

Pycnodothis Stevens n. gen.

Fungus superficial, penetrating the epidermis by haustoria. Pycnidia in stromata. Spores colored, 1-celled. Like Haplosporella Speg. but superficial.

45. Pycnodothis tetracerae Stevens n. sp.

[Figures 78, 79, 108]

Stromata superficial, hypophyllous, surrounded by a scant superficial mycelium. Stromata about 2 mm. in diameter, circular, flat, about 35μ thick, usually bearing the pycnidia in a circle around a sterile center. Pycnidia 30 to 40 or more on one stroma, black, globose, smooth, astomate, about 90 to 108μ in diameter, wall 18μ thick. Spores ovate, honey-yellow, continuous, 7 to 10 x 2μ.

On *Tetracera* sp.

British Guiana: Demerara-Essequibo R. R., July 15, 1922, *408*.

In its strictly superficial habit with small haustoria like those of Meliola, and spherical pycnidia with no ostioles this fungus has a typically perisporiaceous aspect and it doubtless is an imperfect form of such.

CAPNODIACEAE

Polystomellopsis Stevens, n. gen.

Mycelium superficial, yellow, gelatinous. Stromata superficial, nonradiate, many-ostiolate, many-loculate, setose. Asci 8-spored. Spores dark.

46. Polystomellopsis mirabilis Stevens n. sp.

[Figures 80 to 87, 109 to 113]

Stromata hypophyllous, superficial, irregular-oblong, 120 to 400 x 185 to 620μ across, 65 to 70μ thick, bearing numerous setae especially around the edges. Setae black, 60 to 184μ long, straight or irregular, curved, obtuse. Ostioles numerous, 1 to 31, but usually about 10, about 2μ in diameter, Locules many, separated by a gelatinous matrix. Asci 8-spored. Paraphyses filamentous, thin, irregular, gelatinous; spores yellow to brown, oval, continuous, later muriform, 18 to 21 x 11μ. Mycelium superficial, yellow to brown, non-hyphopodiate; mycelial setae few, black, 80 to 180μ long, 7 to 11μ thick at base, irregular in contour.

On *Hirtella* sp.

British Guiana: Kartabo, July 24, 1922, *647* (type); July 21, 1922, *484*; July 23, 1922, *595;* Trinidad: Cumuto, August 16, 1922, *943*.

On *Coccoloba* sp.

British Guiana: Tumatumari, July 8, 1922, *40*.

On unknown host.

British Guiana: Tumatumari, July 8, 1922, *45*.

The colonies of this fungus are approximately circular, Fig. 109, the mycelium radiating from a central point of origin, which point is usually, perhaps always, occupied by a dense aggregate of mycelium (the umbo), (Figure 80), appearing somewhat like a stroma but always devoid of cavities or spores; though on crushing, the mass is seen to be filled with coarse amorphous grains not found elsewhere with the fungus. The mycelium reaches out from this point to a distance of 1 to1.5 cm. and consists, near the center, of thick ropy strands composed of many agglutinated threads. Toward the edge of the colony these strands become smaller, ending in single filaments. (Figure 87). In the lacunae between the ropy strands many thin branches of this mycelium wander. The mycelium appears of somewhat gelatinous texture, particularly evident in the young thin threads and where adjacent strands adhere firmly.

Near the center of a colony are borne from few to several dozen stromata as described above. These always arise in the lacunae between the ropy strands and are produced by the massing of the fine gelatinous threads. The stroma in its very young stages appears to be nearly of its full, mature diameter though very thin and almost translucent and when very young it shows a full compliment of ostioles. Later development consists chiefly in the increase in thickness, color and in the growth of the numerous setae, together with internal development. On crushing the numerous asci and spores are found surrounded with quantities of gelatinous paraphyses. The central umbo lifts readily from the leaf surface and appears to be not at all, or at most very slightly connected with it. Under the umbo there is always a nectary gland, strictly circular, brown, about 385μ in diameter. (Figure 80). Several other species of fungi are found occupying these glands, but no other bore spores. It seems probable that the glands serve as necessary starting points for the growth of the colony. The same relation to glands was noted on the unknown host No. 45, also on the Coccoloba, No. 40.

While the fungus on Coccoloba in the microscopic structure appears to be identical with that on other hosts, microscopically it shows some differences in that the colonies are very much smaller, usually not more than 0.5 cm. in diameter and the number of stromata is less. Evidently the Coccoloba glands do not afford as good conditions regarding nutriment as does Hirtella. This fungus in its perithecium superficially resembles the genus Polystomella of Spegazzini but it cannot be regarded as even of close kinship with that fungus because its perithecium is not radiate; a character which is attributed to Polystomella by all who have worked with the genus (cf. Arnaud[14] Pl. 23 figs. A-K, Theissen,[15] Tab. 6 fig. 4, 13.) and

[14] Arnaud, G. Les Asterinées, Ann. de l'Ecole nat. d'Agric. de Montpellier, 1918.

[15] Theissen, F. Uber Polystomella, Microcyclus u. a. Ann. Myc., 12:63, 1914.

is made distinctive of the Polystomellaceae by Theissen and Sydow[16]. Moreover the mode of origin of the perithecium by anastomosis of many fine mycelial threads is not characteristic of the Microthyriaceae or of the Dothideales.

The peculiar mycelial characters shown are also characteristic of neither of the above named groups. The stromata are Dothideaceous in character in that several locules occur in one stroma each locule without a definite individual perithecial wall; but the mycelium and the appearance of the fungus in general deny relation with the Dothids.

If uniloculate stroma were present there would be no hesitation in placing the fungus in the Capnodiaceae. Pluriloculate stromata in the Capnodiaceae seem somewhat anomolous but are not necessarily so. While this fungus typically has many locules, instances are seen with only one locule. The gelatinous mycelium and the abundant gelatinous paraphyses suggest kinship with the Capnodiaceae and it is in this group that I place it.

There is sufficient resemblance between this fungus and *Chaetoplaca memecycli* Syd.[17] to make it appear that the two may belong in the same family though they clearly do not belong to the same genus owing to the well defined locules in my fungus, such locules being absent in Chaetoplaca. There are also very essential differences in the spore structure. Sydow in his first publication placed his fungus in the Hemisphaeriaceae though latter Theissen and Sydow[18] suggest that it be regarded as a borderland form between the Hemisphaeriaceae and the Discomycetes though they are in doubt whether the whole ascogenous layer represents a disc or whether the structure should be regarded as representing numerous locules each with one ascus.

CLYPEOSPHAERIACEAE

Stegastroma Sydow.

Ann. Myc., 14:81, 1916.

47. Stegastroma guianense Stevens s. p.

[Figures 88, 89]

Spots small, often on the base of the leaflets, pale yellow, bearing several scattered perithecia. Clypeus only in the upper surface, about 30 to 145μ thick and only about 100 to 200μ across. Locules 150 to 260μ in diameter, 170μ deep, ostiole through the clypeus, (7μ). Asci 8-spored, 87 x 25μ. Paraphyses few, filiform. Spores inordinate, pale and continuous

[16] Die Dothideales. Ann. Myc., 13:149, 1915.

[17] Sydow, H. & P. Beitrag zur Kenntnis der Pilzeflora der Philippinen-Inseln. Ann. Myc., 15:232, 1917.

[18] Theissen and Sydow, Syn. Taf. l. c.

when young, 11 to 14 x 7μ, black, 1-septate with a pale band across each cell when mature. One end slightly larger than the other.

On a mimosa-like Legume.

British Guiana: Tumatumari, July 11, 1922, *164.*

The clypeus is strikingly beautiful, being very thick and dark (Fig. 88). and very small in diameter. The perithecial wall and lack of stroma deny relationship with the Dothideales and clearly establish relationship with the Clypeosphaeriaceae and apparently with the genus above named in which there was only one species viz. *S. theisseni* Syd. on Pithecolobium from which ours differs in ostiole, paraphyses, and spore shape.

Anthostomella Sacc.

Consp. Gen Pyren, Ital. System etc. Atti Soc. Ven. Trent, in Padova, 4:1, 1875.

48. Anthostomella rhizomorphae (Kunze) B. and V.

On *Rhizophora mangle.*

British Guiana: Kartabo, July 25, 1922, *643.*

This fungus was originally described as on coriaceous leaves collected in Suriname and has since been collected by the writer in Porto Rico.[19]

49. Anthostomella cecropiae (Rehm) v. Höhn

Ann. Myc. 13:300, 1915.

Auerswaldia cecropiae P. Henn. Hedw., 23:253, 1904.

Physalospora cecropiae Rehm, Hedw., 40:112, 1901.

On *Cecropia* sps.

British Guiana: Tumatumari, July 12, 1922, *223*; Demerara-Essequibo R. R., July 15, 1922. *397, 403, 118.*

[19] Bot. Gaz., 70. 399, 1920.

PLATE I

EXPLANATION OF PLATES

PLATE I

Figs. 1–4 *Hysterostromina palmae.*

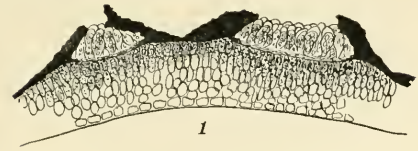
Fig. 1. Two perithecia in section showing location and relation to the tissues.
Fig. 2. Edge of a perithecium showing radiate character and absence of free mycelium.
Fig. 3. Edge of perithecium showing more detail, also 3-ascospores.
Fig. 4. Two asci with spores.

Figs. 5, 6 *Coccostromopsis palmigena.*

Fig. 5. A stroma in section showing locules and central attachment.
Fig. 6. An ascus with spores.

Figs. 7–14 *Nowellia guianensis.*

Fig. 7. Drawing of a stroma in section showing foot and two locules.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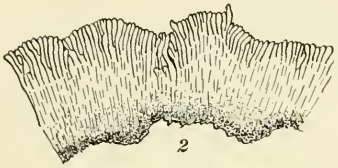
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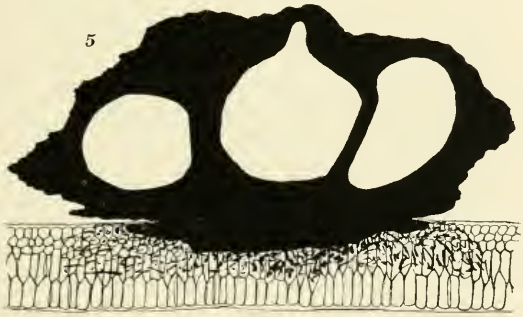
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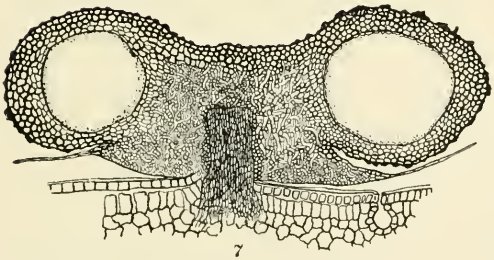
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STEVENS PARASITIC FUNGI PLATE I

PLATE II

PLATE II

Fig. 8. Drawing of an ascus and spores.
Fig. 9. Two spores showing the gelatinous envelope.
Fig. 10. Edge of colony showing irregular radiation and erose margin.
Fig. 11. Detail of cell structure of foot and adjacent stroma.
Fig. 12. Detail of covering of the loculi showing dark, thick-walled outer layer and pale hymenial layer.
Fig. 13. Diagram showing three stromata close together.
Fig. 14. Diagram showing two stromata fused.

Figs. 15, 16 *Leveillinopsis palmicola*

Fig. 15. Section of a stroma showing its superficial character.
Fig. 16. An ascus and spores.

Figs. 17–19 *Amerodothis guianensis.*

Fig. 17. Diagram of stromata in section showing the locules and the variation in the position of the stromata.
Fig. 18. An ascus and spores.

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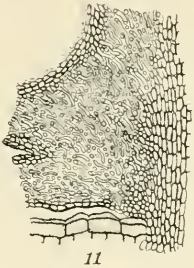
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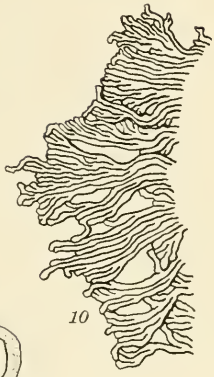
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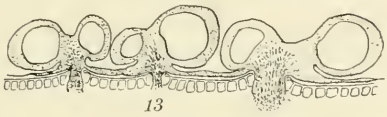
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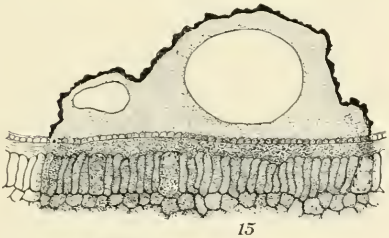
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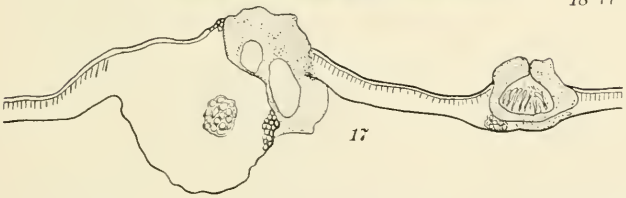
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STEVENS PARASITIC FUNGI PLATE II

PLATE III

PLATE III

Fig. 19. Spores.

Figs. 20–23 *Uleodothis paspali.*

Fig. 20. Section of a stroma showing four locules and the irregular stroma extending to the lower epidermis.

Fig. 21. Section of a uniloculate stroma.

Fig. 22. An ascus.

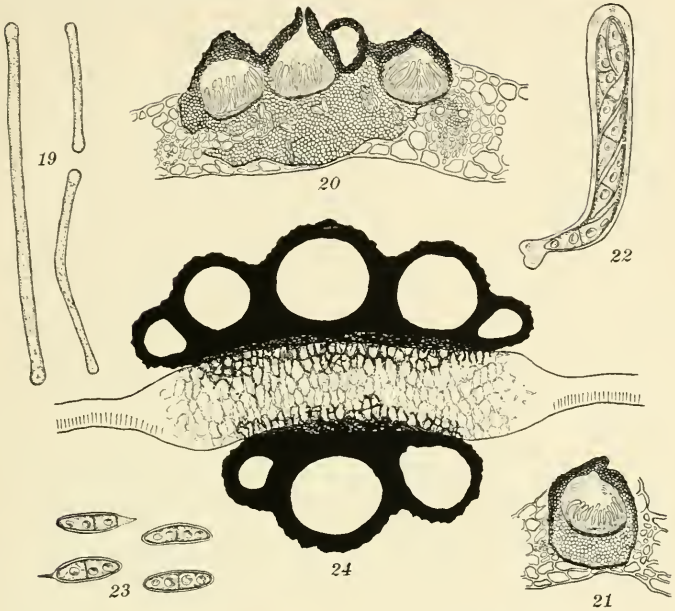
Fig. 23. Ascospores.

Figs. 24–27 *Achorella guianensis.*

Fig. 24. Diagram to show the relation of the locules to the stroma and the hypostroma.

Fig. 25. A locule in stromatic tissue showing the dothideoid character.

Fig. 26. Detail of hypostroma as it occurs in the mesophyll.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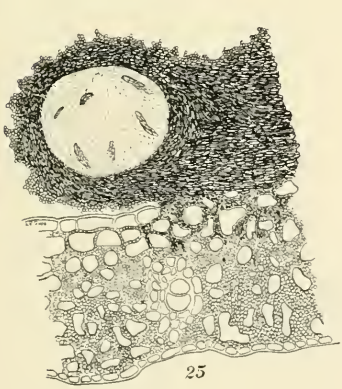
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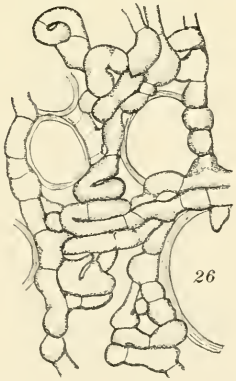
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PLATE IV

PLATE IV

Fig. 27. An ascus, paraphyses and spores.

Figs. 28–31 *Anisochora tabebuiae.*

Fig. 28. Cross section of a leaf showing palisade stroma, epidermal clypeus, infected phloem, a locule with ostiole.

Fig. 29. Diagram of a section of a stroma showing three locules.

Fig. 30. Detail of a portion of stroma and clypeus showing the hyphal nature of the stroma.

Fig. 31. An ascus with spores, and a single spore.

Figs. 32–34 *Scolecodothopsis ingae.*

Fig. 32. Section of a stroma showing three locules with asci.

Fig. 33. An ascus with spores.

Fig. 34. Three spores showing shape and septation.

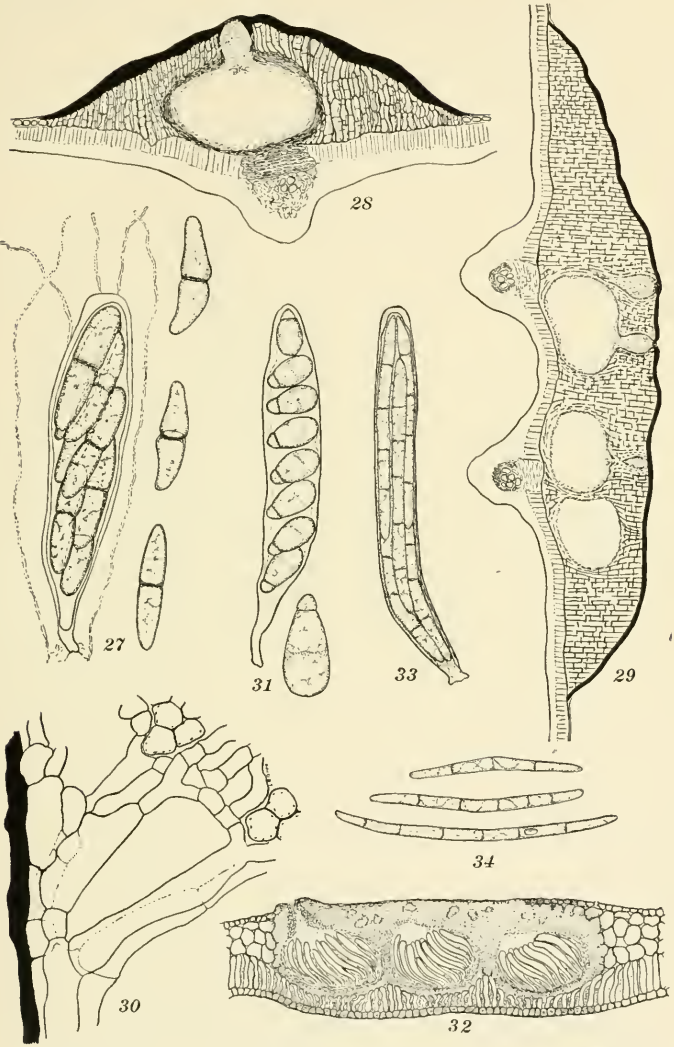
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PLATE V

PLATE V

Fig. 35. *Phyllachora aegiphilae.* An ascus with spores, also three spores.

Figs. 36–38 *Phyllachora chaetochloae.*

Fig. 36. An ascus with spores and paraphyses.
Fig. 37. Filiform conidia.
Fig. 38. Five of the oblong conidia.

Figs. 39–41 *Phyllachora dimorphandrae.*

Fig. 39. Diagrammatic drawing to show position and shape of locules in the stroma.
Fig. 40. Detail of a portion of a locule showing the lining membrane.
Fig. 41. Ascus and spores.

Figs. 42–43 *Phyllachora tabernaemontanae*

Fig. 42. Diagram showing position of the locules in the leaf.
Fig. 43, 43a. Asci paraphyses and spores.

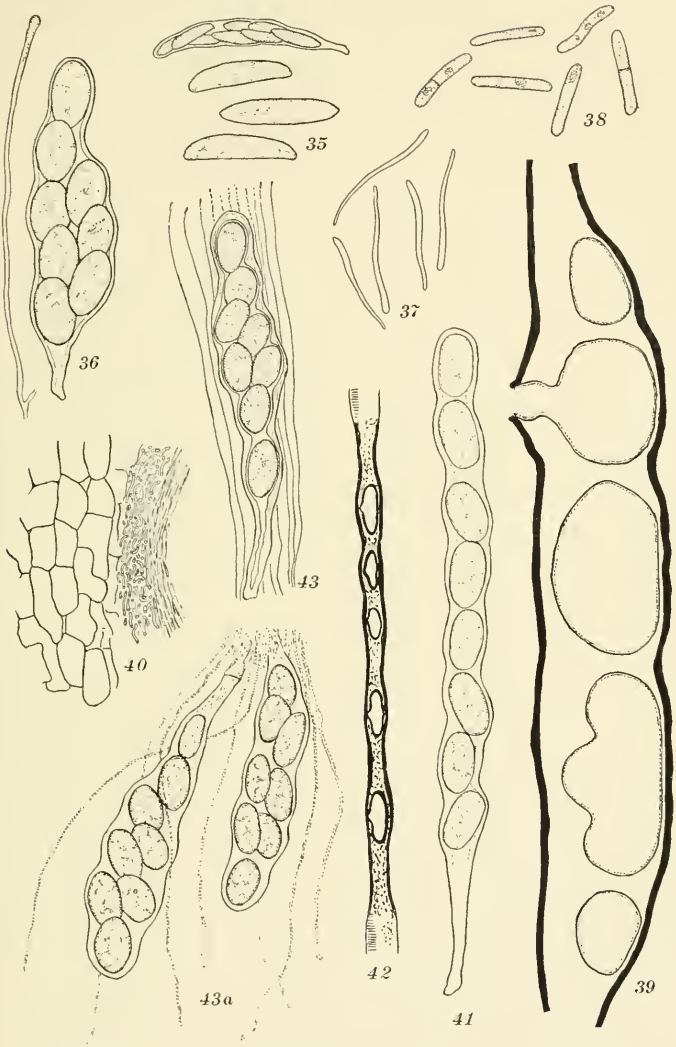
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PLATE VI

PLATE VI

Figs. 44–46 *Phyllachora tiliae.*

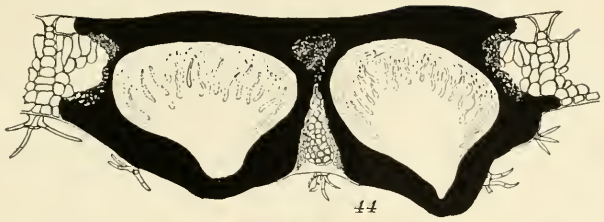
Fig. 44. A stroma with two locules.
Fig. 45. An ascus with spores.
Fig. 46. Two spores.

Figs. 47–50 *Phyllachora wismarensis.*

Fig. 47. A stroma showing three locules.
Fig. 48. An ascus and spores.
Fig. 49. Two spores.
Fig. 50. Filiform conidia.
Fig. 51. *Phyllachora* No. 1, Diagram of stroma and locules.

Figs. 52–54 *Phyllachora* No. 2.

Fig. 52. A perithecium showing clypeus.
Fig. 53. A pycnidium showing conidia.
Fig. 54. A stroma with two locules.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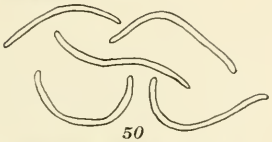
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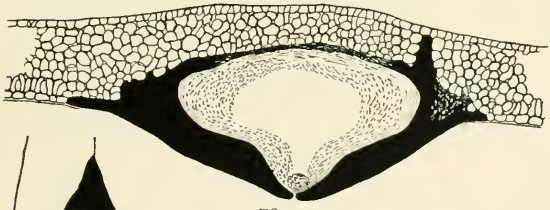
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PLATE VII

PLATE VII

Fig. 55. *Phyllachora* No. 5, Stroma in section showing the upper and lower clypeus and the way it envelops the locule.

Fig. 56. *Endodothella anacardiacearum.* Section of stroma showing position of the locules.

Figs. 57–59 *Endodothella tapirae.*

Fig. 57. A stroma occupying one side of the leaf only.

Fig. 58. A stroma occupying both sides of the leaf with much increase in thickness.

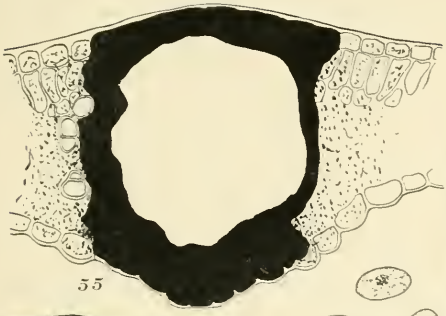
Fig. 59. Detail of a portion of the stroma shown in fig. 58 showing character of the stroma and deformation of the host tissue.

Figs. 60–62 *Haplothecium guianense.*

Fig. 60. Section of a stroma showing six locules, the upper and lower clypeus, the diseased palisade cells and the position of the loose stroma in the mesophyll.

Fig. 61. An ascus.

Fig. 62. Spores.



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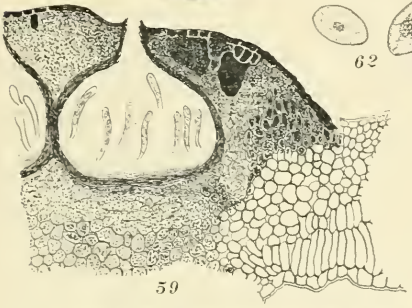

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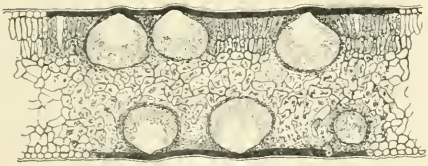

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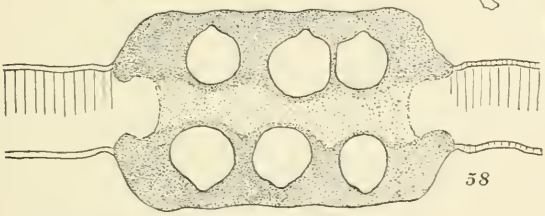

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PLATE VIII

PLATE VIII

Figs. 63–65 *Gymnopeltis trinidadensis.*

Fig. 63. An ascoma on the leaf surface showing scattered naked asci.
Fig. 64. Three asci.
Fig. 65. Two asco-spores.

Figs. 66–67 *Meliolinopsis palmicola.*

Fig. 66. A bit of mycelium; a setum and tip of a setum.
Fig. 67. A spore.

Figs. 68–70 *Hyalomeliolina guianensis.*

Fig. 68. A perithecium in section.
Fig. 69. Mycelium showing the tendency to mass together in ropes.

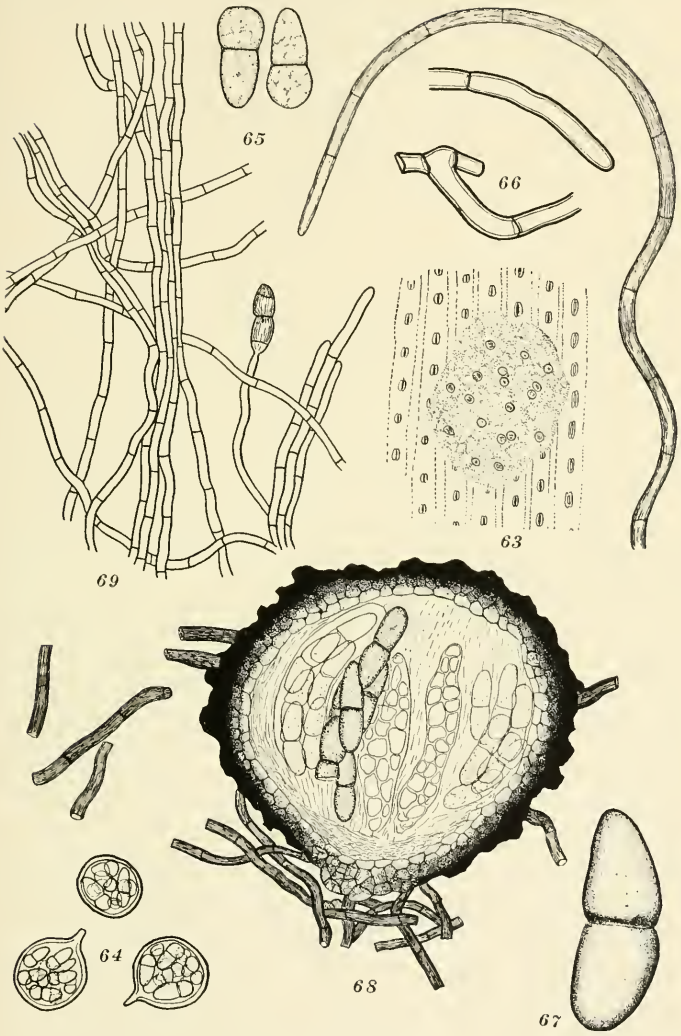
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PLATE IX

PLATE IX

Fig. 70. Spores showing septation and germination.

Figs. 71–76 *Haraea mauritiae.*

Fig. 71. A perithecium with setae.
Fig. 72. An ascus with spores.
Fig. 73. Two spores; 1-septate and 2-septate.
Fig. 74. Perithecial setae.
Fig. 75. Mycelium.
Fig. 76. Three pseudohyphopodia.
Fig. 77. *Dimerium guianense.* Three spores.

Figs. 78–79 *Pycnodothis tetracerae.*

Fig. 78. A stroma showing locules.
Fig. 79. Diagram showing position of the locules in a stroma.

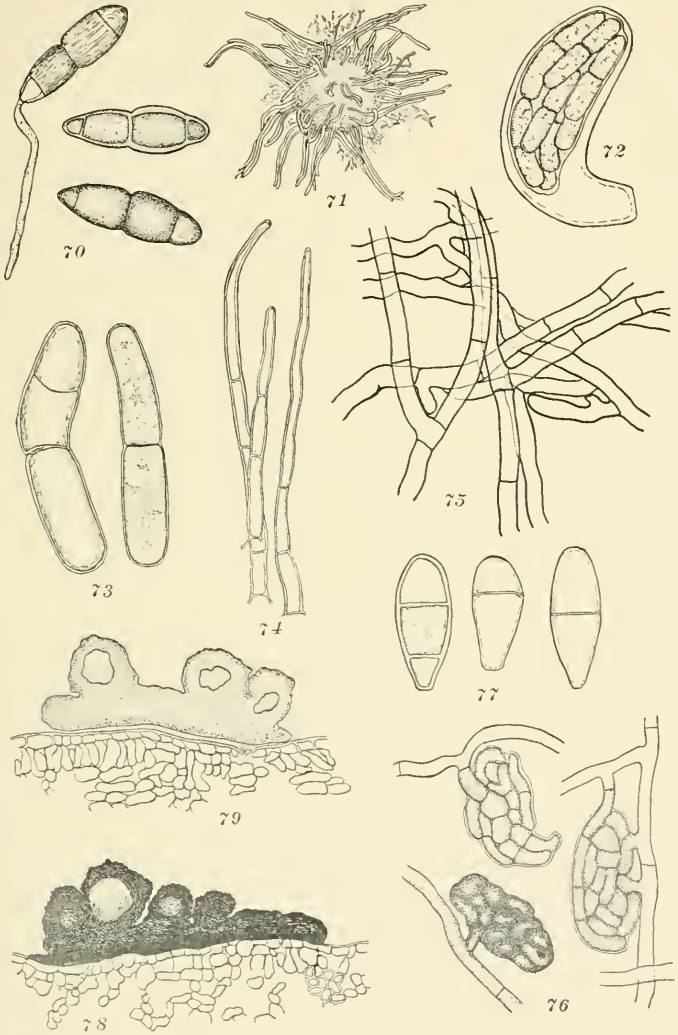

70
71
72
73
74
75
77
78
79
76

PLATE X

PLATE X

Figs. 80–87 *Polystomellopsis mirabilis.*

Fig. 80. Section of a nectary gland showing the umbo resting on it. The black represents the region occupied by the fungus.
Fig. 81. Sections of stromata showing dark cover, setae, locules resting in a gelatinous matrix.
Fig. 82. Detail of ostiole and mesh of surface cover showing that it is non-radiate.
Fig. 83. Diagram of a stroma viewed from above showing mycelium, setae and ostioles.
Fig. 84. Two perithecial setae.

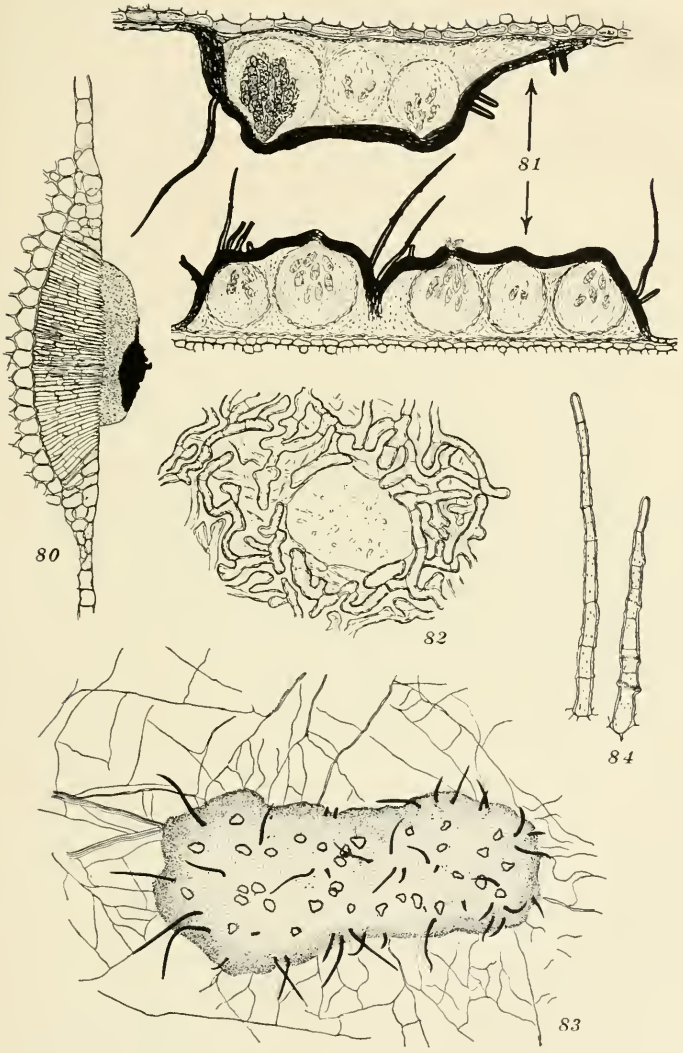

81
80
82
84
83

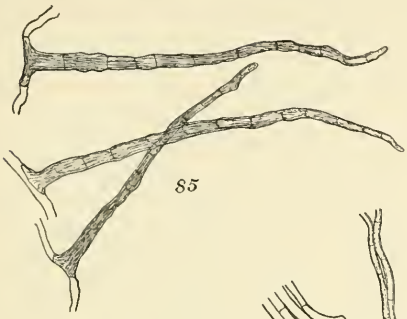
PLATE XI

PLATE XI

Fig. 85. Setae showing attachment to mycelium.
Fig. 86. Spores.
Fig. 87. Mycelial ropes, also mycelium in less dense aggregations.

Figs. 88–89 *Stegastroma guianense.*

Fig. 88. Section of two perithecia showing the cavity, the epiphyllous clypeus and the perithecial wall.
Fig. 89. A spore.



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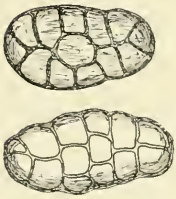
89



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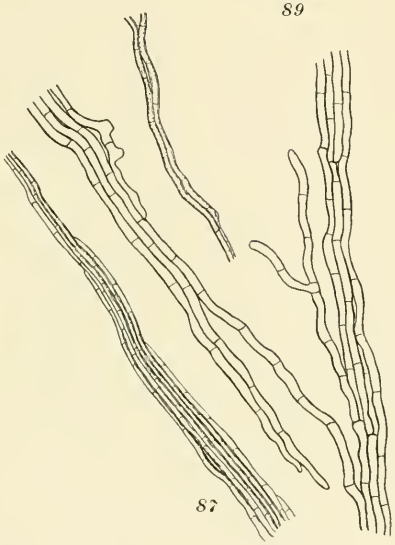


87

88

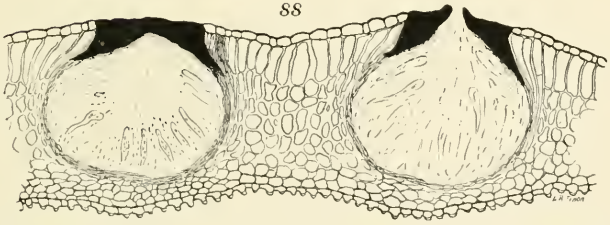


PLATE XII

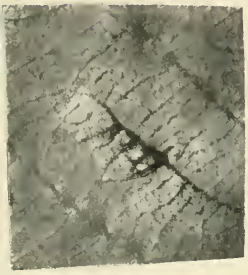
PLATE XII

Fig. 90. *Amerodothis guianensis.* Photograph of a leaf spot from above, enlarged showing stromata on the veins.

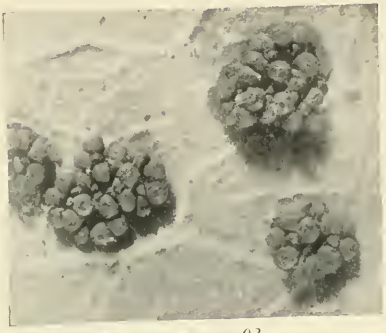
Figs. 91–92 *Achorella guianensis.*

Fig. 91. Photograph of a leaf showing numerous groups of perithecia. Actual length of leaf as shown 21 cm.

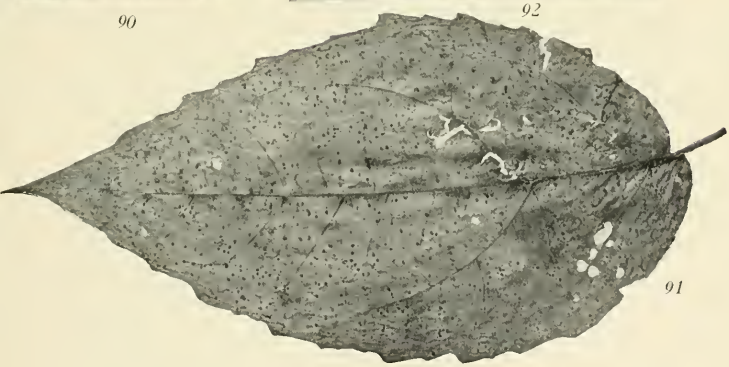
Fig. 92. Photograph of groups of perithecia on a stroma.



90



92



91

PLATE XIII

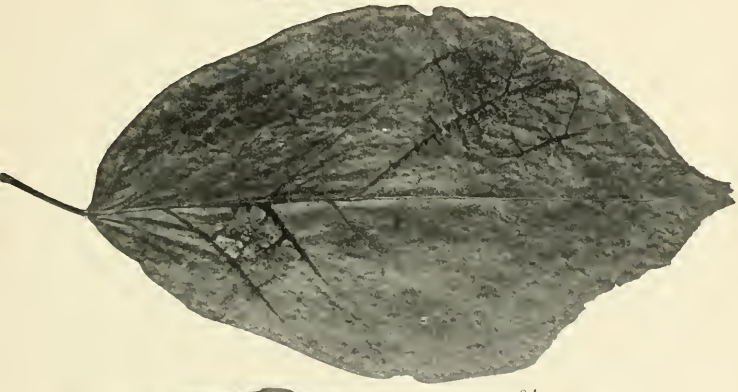
PLATE XIII

Fig. 93. *Nowellia guianensis*. Photograph of a leaf showing general distribution and appearance of the stromata. Actual length of leaf as shown 9.5 cm.

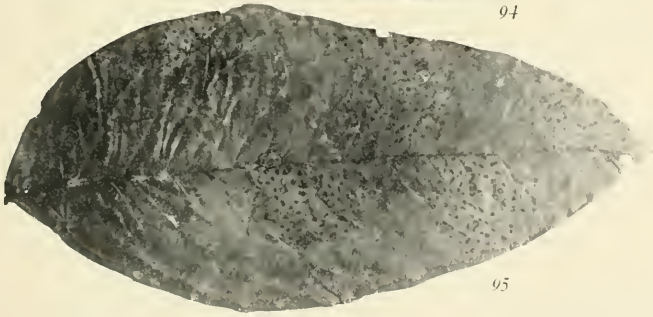
Fig. 94. *Anisochora tabebuiae*. Photograph of a leaf showing two spots and the stromata following the veins. Actual length of leaf as shown 15 cm.

Fig. 95. *Scolecodothopsis ingae*. Photograph showing spots and stromata. Actual size of leaf as shown 17.8 cm.

93



94



95

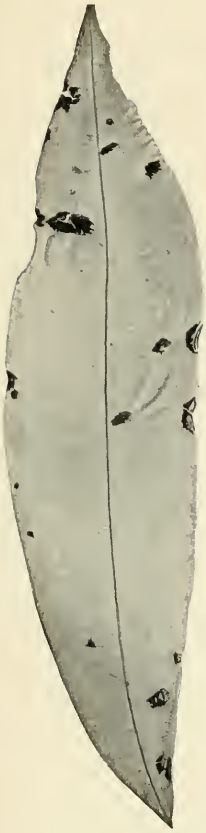
PLATE XIV

PLATE XIV

Fig. 96. *Phyllachora dimorphandrae.* Photograph of a leaflet showing stromata and leaf shape. Actual length of leaflet as shown 28 cm.

Fig. 97. *Phyllachora chaetochloae.* Photograph showing stromata.

Fig. 98. *Phyllachora tabernaemontanae.* A leaf showing stromata. Actual length of leaf as shown 20.3 cm.



96

97

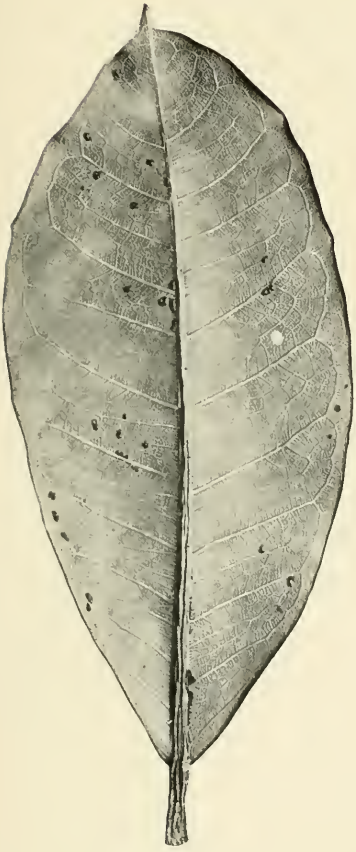
98

PLATE XV

PLATE XV

Fig. 99. *Phyllachora wismarensis*. Photograph of leaf showing stromata. Actual length of leaf as shown 17.6 cm.

Fig. 100. *Phyllachora* No. 2. Photograph of leaf showing stromata. Actual length of leaf as shown 30.5 cm.



99

100

PLATE XVI

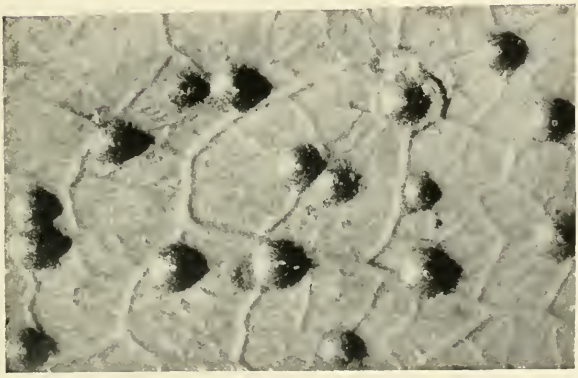
PLATE XVI

Fig. 101. *Phyllachora* No. 4. Photograph of leaves showing character of the spot, stromata and of the host. Actual length of stem as shown 9. cm.

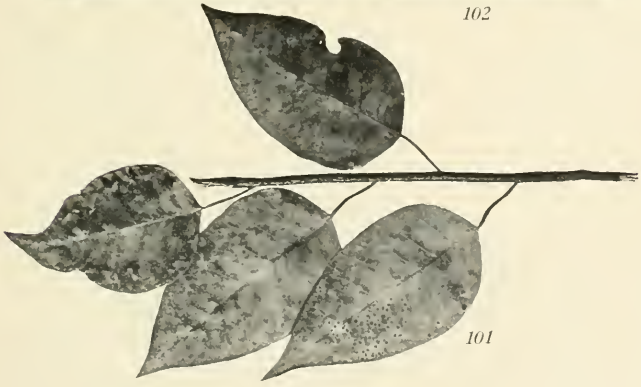
Fig. 102. A portion of the leaf shown in fig. 100 enlarged to show the stromata.

Fig. 103. *Phyllachora* No. 6 showing stromata and host. Actual length of stem shown 9 cm.

103



102



101

PLATE XVII

PLATE XVII

Fig. 104. *Haplothecium guianense.* Photograph of leaflet showing stromata, also four Meliola colonies. Actual length of leaf as shown 13.3 cm.

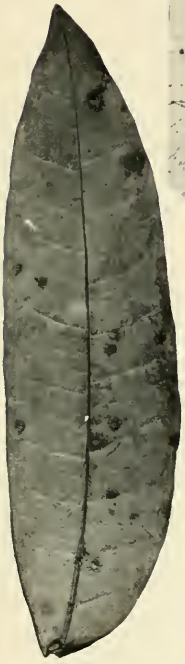
Figs. 105–106 *Hyalomeliolina guianensis.*

Fig. 105. A leaf showing several colonies. Actual length of leaf 12.3 cm.

Fig. 106. A colony magnified and showing the character of the mycelium.

Fig. 107. *Dimerium guianense.* Photograph showing colonies. Length of leaf 10.5 cm.

106



104 107 105

PLATE XVIII

PLATE XVIII

Figs. 109–113 *Polystomellopsis mirabilis.*

Fig. 109. Photograph of a leaf showing colony.

Fig. 110. Photomicrograph giving a general view of the center of a colony showing the central umbo, the radiating ropy mycelium and several stromata.

109

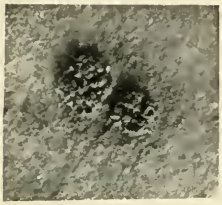
110

PLATE XIX

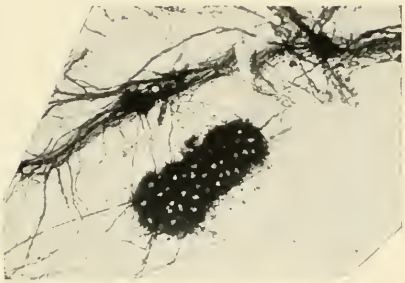
PLATE XIX

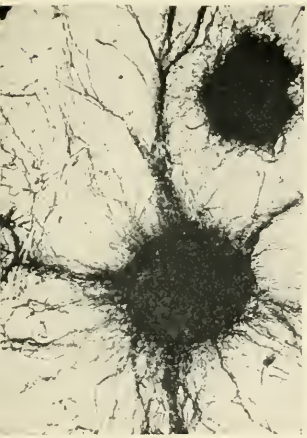
Fig. 111. Photomicrograph of an umbo with radiating mycelium and one young stroma.
Fig. 112. Photomicrograph showing mycelium and several stromata.
Fig. 113. Photomicrograph of a single stroma showing numerous ostioles.
Fig. 108. *Pycnodothis tetracerae.* Enlarged view of stromata.

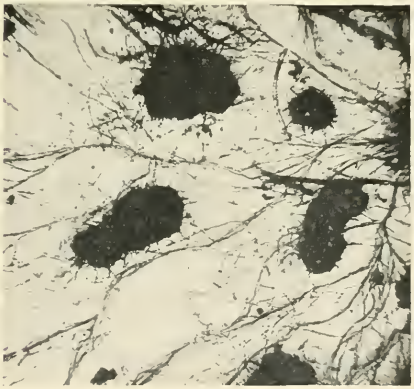
108



113







111

112

INDEX TO SPECIES

Achorella guianensis 15
Amerodothis guianensis 14
Anisochora tabebuiae 16
Anthostomella cecropiae 35
Anthostomella rhizomorphae 35
Bagnisiopsis peribebuycnsis 13
Coccostromopsis palmigena 10
Dimeriella cordiae 27
Dimeriella erigeronicola 26
Dimerium guianense 31
Endodothella anacardiacearum 24
Endodothella tapirae 24
Gymnopeltis trinidadensis 26
Haplothecium guianense 25
Haraea mauritiae 29
Hyalomeliolina guianensis 28
Hysterostomina palmae 10
Leveillinopsis palmicola 13
Meliolinopsis palmicola 27
Mycophaga guianensis 31
Nowellia guianensis 11
Oplothecium palmae 28
Parodiopsis ingarum 30
Parodiopsis melioloides 29
Parodiopsis sp. ind. 30
Parodiopsis viridescens 30
Phaeodimeriella asterinarum 27
Phyllachora aegiphilae 18
Phyllachora chaetochloae 18
Phyllachora congruens 19
Phyllachora dimorphandrae 19
Phyllachora englri 19
Phyllachora guianensis 19
Phyllachora Nos. 1-6 22–24
Phyllachora paspalicola 20
Phyllachora phaseoli 20
Phyllachora tabernaemontanae 20
Phyllachora tiliae 21
Phyllachora ulei 21
Phyllachora wismarensis 21
Polystomellopsis mirabilis 32
Pycnodothis tetracerae 32
Scolecodothopsis ingae 17
Stegastroma guianense 34
Uleodothis paspali 15

INDEX TO HOSTS

Aegiphila..... 18
Alchornea cordata..... 29
Anacardiaceae..... 24
Anacardium..... 31
Anonaceae..... 27
Anthurium..... 19
Apocynaceae..... 30
Bactris..... 27
Banisteria ciliata..... 30
Cecropia..... 35
Celastraceae..... 11
Chaetochloa tenax..... 18
Coccoloba..... 32
Cordia..... 27
Dimorphandra..... 19
Dioscorea..... 21
Erigeron bonariensis..... 26
Ficus..... 21
Hirtella..... 32
Inga..... 17, 30
Legume..... 20, 23, 35
Licania..... 28
Mauritia..... 29
Melastomataceae..... 13
Microthyriaceae..... 27
Mikania (?)..... 16
Palm..... 10, 11, 13, 28
Paspalum arenarum..... 20
Paspalum conjugatum..... 15, 20
Paspalum virgatum..... 20
Rhizophora mangle..... 35
Rosaceae..... 52
Tabebuia..... 16
Tabernaemontana..... 20
Tapira..... 24
Tetracera..... 32
Tiliaceae..... 21
Unknown host..... 22, 23, 24, 25
Valota laxa..... 19

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THE EXTERNAL MORPHOLOGY AND POSTEMBRYOLOGY OF NOCTUID LARVAE

WITH EIGHT PLATES

BY
LEWIS BRADFORD RIPLEY

Contribution from the
Entomological Laboratories of the University of Illinois
No. 86

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN
ENTOMOLOGY IN THE GRADUATE SCHOOL OF
THE UNIVERSITY OF ILLINOIS

1921

TABLE OF CONTENTS

Introduction 7
Larval Morphology 9
Fixed Parts of the Head 9
Endoskeleton 12
Movable Parts of the Head 15
Spinneret 19
Prepharynx 25
Setae of Trunk 27
Larvapods 34
Postembryology 37
Number of Molts 37
Postembryonic Changes 43
Adfrontal Sutures 46
Epicranial Stem 47
Determination of Burrowing Habit 49
Resistance to Submergence 52
Epicranial Index and Subterranean Habit 56
Postembryology of Labium and Spinneret 69
Larvapods 75
Crochets 79
Summary 80
Postscript 82
Bibliography 83
Explanation of Plates 87

INTRODUCTION

The principal object sought in this work is to investigate the value of certain more or less neglected lines of evidence as a source of phylogenetic information. Such evidence has been applied to the Noctuidae for the purpose of throwing light upon our knowledge of the structural and biological relationships within the family. It has also been our aim to perform the necessary studies preliminary to the making of natural tables for the identification of noctuid larvae.

There are four kinds of evidence contributing to our knowledge of the phylogeny of animals: comparative anatomical, recapitulative, paleontological, and biological. Heretofore the systematic entomologist has concerned himself almost entirely with the first of these, the second remaining either uninvestigated or uninterpreted, the third presenting a relatively scant amount of material, and the last offering a virtually untouched field of somewhat uncertain possibility. Not only has the worker on the taxonomy of insects practically confined himself to anatomical evidence, but he has, until quite recently, based his classification solely on the structure of adult insects. Within the last decade a few excellent researches on the classification of immature insects, such as Fracker's upon lepidopterous larvae, Howard, Dyar, and Knab's upon mosquito larvae, Edna Mosher's upon the taxonomy of lepidopterous pupae, and Malloch's studies upon immature Diptera, have demonstrated beyond a doubt the value of a morphological study of immature insects as a source of phylogenetic information.

The study of the ontogeny of insects may be conveniently divided into embryology and postembryology. The latter deals with development after hatching from the egg. It regards the larva as a free-living embryo, and the pupa as representing a highly specialized stage corresponding to a larval stadium. We may, then, speak of larval or pupal postembryology.

Since the earlier embryonic stages of insects must recapitulate, so far as the law is manifested, conditions in phylogeny prior to the appearance of insects, the taxonomist must look to the older embryonic stages, which have usually not been studied, and to the postembryonic development for recapitulative evidence. As might be expected from their highly adaptive nature, pupae reveal the working of recapitulation to a less marked extent than do larvae. Comstock, however, based his hypothetical ancestral wing venation upon the pupal wing of Hepialus, and Dr. Edna Mosher found that certain wingless female moths have pupal wing-pads. In

general, larval postembryology may reasonably be regarded as the principal source of recapitulative evidence to be applied within families or smaller groups. A study of the later embryonic stages may, on the other hand, be expected to throw light upon the relationships between families and orders.

Biology, although never serving as a basis for classification, under our present system, quite frequently furnishes evidence of a corroborative nature. For example, the peculiar scattered distribution of Peripatus is regarded as an indication of great phylogenetic antiquity. Physiological life-history in relation to taxonomy has been studied but little. Since various types of life-history are often found within closely related groups, no marked correlation is generally evident; however, when the evolution of life-history becomes better understood, it seems quite possible that our sources of phylogenetic knowledge will be further supplemented by a study of physiological life-history.

This consideration of the sources of our taxonomic knowledge with reference to their development in entomology may be summarized thus: the comparative morphology of the immature stages presents a relatively new field of well established systematic value; recapitulation offers a practically unexplored source of information of considerable promise, and biology may yield valuable evidence from the taxonomic point of view.

In a systematic treatment of an unsatisfactorily classified group all evidence available should be sought. It is to be expected that neglected sources of information will first be called into use in those difficult groups where the morphology of the adults alone has not been sufficient to bring about a satisfactory understanding of relationships. The Noctuidae represent such a group. With its 3500 North American species, its many ill-defined genera, its striking structural uniformity, and its large number of extremely variable species, we are not surprised to find that systematists have had considerable difficulty with this family. A large proportion of the misnamed and unnamed Lepidoptera in collections belong to the Noctuidae. Its general importance is probably not surpassed by that of any other family of insects, containing, as it does, about one-half of the described Lepidoptera of North America. The great economic importance of the Noctuidae needs only to be mentioned.

It is hoped that the following contribution to the larval postembryology, larval morphology, and general biology of the Noctuidae may not only demonstrate the general value of these more or less neglected sources of phylogenetic evidence, but may also present, in a preliminary manner, their application to the solving of some of the many problems of the evolution of structure and habit within the family.

LARVAL MORPHOLOGY

Noctuid larvae, with the exception of a few genera, are characterized by their marked uniformity of structure. Of these the genus Acronycta and its allies, whose larvae resemble those of the arctiids, with their characteristic tufts of setae, has been treated by Dyar to the number of about fifty species. The larvae of certain other genera look like those of the Geometridae, lacking one or two pairs of larvapods. For the greater part, however, noctuid larvae are uniform with regard to most of the characters used by Fracker in his key to lepidopterous larvae. The position of body-setae, for instance, the taxonomic value of which was early pointed out by Dyar and which plays an important rôle in Fracker's work, is very nearly uniform thruout the family. The same may be said of the arrangement of the crochets. Certain head-structures, however, first emphasized by Forbes, are variable within the Noctuidae. Crumb, in his key to cut-worms injurious to tobacco, used various types of skin-sculpture, the microscopic structure of the cuticle of the body. The conspicuous variation in the number of larvapods has, of course, long been known. With the exception of Dyar's monograph of Acronycta and its allies, and Crumb's artificial key for the identification of fourteen species of tobacco cut-worms, we have no works dealing with the classification of noctuid larvae. Fracker, however, gives characters for separating the family from all others but the Agaristidae. He divides it into four groups, all of which are listed in different places in his table. The following morphological study has been made to determine the taxonomic value of the structural variation which this family exhibits in its larvae, as well as to provide the basis for a post-embryological study of the group.

FIXED PARTS OF THE HEAD

Since the structure of the head (Figs. 1–17) of noctuid larvae does not differ fundamentally from that typical of the entire order, the morphological treatment which follows applies for the most part to lepidopterous larvae in general. The epicranial suture assumes the form of an inverted Y (Fig. 2) with the stem following the dorsal portion of the meson and the two arms extending ventrolaterad on either side. Since the epicranial stem represents the median line of dorsal closure in the embryo, the arms being derived from the closure on either side of the so-called unpaired appendage, the homology of this suture with that of the larvae of all other orders is unquestionable. In nymphs or adults of the Orthoptera the

antacoriae divide each epicranial arm into two portions, the ventral being known as the fronto-genal suture. These are homologous, therefore, with the ventral portions of the epicranial arms of larvae. The two large sclerites which are separated by the epicranial stem, lie dorsad of the arms, comprise the greater part of the head-capsule, and make up the vertex. Its apparent large size in larvae is due to the absence of compound eyes. Since the occipital sutures are undeveloped, the caudal extent of the vertex is indefinite. It has been customary to refer to the fused vertex, occiput and postgenae as the epicranium. The vertex of lepidopterous larvae does not differ from larval vertices generally in bearing the ocellarae, and antennarae. The antennarae, which bear the antennae, are distinct in the noctuid larvae, a generalized condition found typically in the adults of the more primitive orders.

There is but one marked indication of fundamental structural specialization visible externally on the vertex of lepidopterous larvae. The adfrontal sutures, which have developed solely in the larvae of this order, run subparallel to the epicranial arms, dividing the vertex on each side into two portions, the mesal one being the well known adfrontal area. Heretofore, these secondary adfrontal sutures have been generally regarded as the epicranial arms and vice versa. Heinrich agrees with Dampf in his assertion that the adfrontal sclerites are a part of the front, regarding the sutures between the front and adfrontals as secondary infoldings. Both of these investigators were aware that the pretentoria invaginate at the bottoms of these infoldings, a point demonstrated by Berlese one year previous to the publication of Dampf's paper on case-bearing larvae. The interpretation of these authors necessitates the supposition that the pretentorinae were originally located on the front some distance mesad of the epicranial arms and that they were subsequently involved by this supposedly secondary infolding, which resulted in their present position. We shall present evidence which appears to show conclusively that the mesal sutures are the epicranial arms and that the lateral ones are secondarily developed.

In the first place, the pretentorinae of the larvae of other orders, so far as we know, are associated with the epicranial arms. They are rarely situated on the front removed from primary sutures. Moreover, the epicranial stem in lepidopterous larvae, unquestionably a primary structure, is followed internally (Fig. 1) by a deep infolding, which is continuous with and exactly like those of the mesal sutures which bear the pretentorinae. It seems highly improbable that the former suture should be primary and the latter secondary, when their infoldings are continuous. The frontoclypeal suture, also a primary suture beyond a doubt, is expressed internally by a similar infolding. This suture extends between the mesal sutures and does not traverse the adfrontal sclerites terminating at the lateral sutures,

as it should if the lateral sutures were the epicranial arms. Postembryological evidence offers still stronger support to this interpretation. The lateral sutures are not distinct in noctuid larvae in instars earlier than the penultimate. So far as we have been able to ascertain the earlier instars of all lepidopterous larvae lack the adfrontal area, although this point appears to have been generally overlooked. It is not always distinctly separated from the vertex even in full grown larvae. The accurate morphologist, Berlese, shows no trace of it in his figures of the ectal and ental aspects of the larval head of *Acherontia*. These are secondary structures appearing relatively late in their postembryonic development. Therefore, they cannot be homologous with the epicranial arms, which represent the lines of dorsal closure on each side of the so-called unpaired appendage in the embryonic development.

The triangular front between the epicranial arms is separated from the postclypeus by a more or less distinct frontoclypeal suture. This suture in the more primitive insects terminates near the precoilae. In lepidopterous larvae this suture has migrated dorsad, its ends joining the epicranial arms at points considerably removed from the articulations of the mandibles, a condition frequently found in specialized insects. Whereas the position of this suture probably denotes specialization, its well developed condition, on the other hand, is to be regarded as a generalization, since it is frequently lost in both larvae and adults of various orders. It is sometimes not traceable externally in noctuid larvae and is rarely as prominent as the clypeal suture, which marks the division between the preclypeus and the postclypeus. This division also denotes a primitive condition, as is evident from a general study of insect morphology. The labrum of the noctuid larva always presents the bilobed shape characteristic of lepidopterous larvae.

The caudal aspect of the lepidopterous larval head shows pronounced and varied specialization. It seems odd that this region, which perhaps offers points of greater morphological interest than any other part of the head, should have been so utterly neglected. Prominent secondary sutures extend dorsad from the mesal edge of the postcoilae, marking the location of deep infoldings. The position of these sutures with reference to the postcoilae precludes their being homologous with the occipital sutures, which are always situated laterad of the postcoilae and are universally borne by the postgenae. It is convenient to refer to the region mesad of these sutures as postgenae, although it should be remembered that the lateral extent of the true postgenae is undefined, the occipital sutures being undeveloped. In all but certain of the more specialized orders the postgenae in both larval and adult insects are widely separated by the cervix. In lepidopterous larvae there has been a tendency toward the extension mesad and an ultimate fusion of the postgenae, resulting in a

separation of the labium from the cervix. Consequently, this appendage is finally borne by the postgenae instead of by the cervix, which represents the segment to which the labium morphologically belongs. A parallel specialization is exhibited by the adults of certain aculeate Hymenoptera.

In the more generalized lepidopterous larvae of the Cossidae, Pyralididae, and Tortricidae examined, a few species of each, we find the postgenae quite widely separated (Figs. 3, 4, 5). Young larvae of *Thyridopteryx ephemeraeformis* from the first to the fourth instars (Fig. 6) also reveal this condition, although these sclerites meet on the meson in the full-grown larvae (Fig. 7), a recapitulation to be treated later in the section on postembryology. Secondary sclerites are sometimes formed by a chitinization of this membrane (Fig. 4). Frequently each postgena (Fig. 5) is divided by an oblique secondary suture. In hesperiid larvae the postgenae are exceptionally widely separated, the area (Fig. 8) between them being uniformly and heavily chitinized, resembling the gula of the Coleoptera. Larvae of several families have retained but a narrow strip of cervacoria between the postgenae. In representatives of the Sphingidae, Saturniidae, Lymantriidae, and Pieridae examined, they are separated only by a suture. The Noctuidae (Figs. 9-12) present the same condition most frequently, although a narrow strip of coria often persists.

In certain of the more specialized families, notably the Saturniidae and Noctuidae, the cervix caudad of the postgenae has developed a varying number of folds, some of which have become flattened one onto the other, chitinized, and cemented to the postgenae, where they now resemble sclerites. This peculiar condition appears to reach its height in the former family, some of whose larvae have several such folds superimposed upon one another and apparently fused into a thick, heavily chitinized sclerite, which lies flat upon the postgenae. In the Noctuidae the most cephalic fold only is chitinized and fastened down in this manner, where it assumes a bilobed form. The dorsal portion of this cervical fold is covered by the membranous one which follows it, exposing the brown, flat, crescent-shaped ends of the bilobed first fold, so that they appear as divisions of the postgenae, one on each side of the meson.

In the Noctuidae part of the secondary infolding which extends around the dorsal portion of the margin of the foramen separates on each side a crescent-shaped secondary sclerite (Fig. 9) from the remainder of the vertex. The pleural portion of the neck-membrane is fastened to this sclerite.

ENDOSKELETON

The tentorium of lepidopterous larvae (Figs. 3, 13, 14) is very greatly reduced. It is unfit for the function of support generally performed by this structure. In correlation with this reduction a large number of large, heavily chitinized infoldings have developed along certain primary and

secondary sutures, comprising the sole endoskeleton functioning as such, the tentorium being not only very vestigeal but to a large extent membranous and flimsy. These secondary infoldings will be referred to as parademes, a term used to designate secondary infoldings in general.

In the order Orthoptera the pretentorinae are always found at the ends of the fronto-clypeal suture, this being probably the most generalized condition. These invaginations have migrated dorsad along the fronto-clypeal suture for a considerable distance in the aculeate Hymenoptera. A similar specialization has developed in the lepidopterous larva in a parallel manner, the pretentorinae being located on the epicranial arms (Fig. 13) usually nearer to the dorsal end of the front than to the clypeus. It is of interest to recall that the condition of the postgenae in these larvae is also parallelled in important respects by that of adult Hymenoptera. The position of the pretentorinae is not externally marked, since they invaginate at the bottoms of the epicranial parademes, large infoldings, which extend throughout the entire length of the epicranial suture. Each ribbon-like pretentorium extends caudad to a metatentorium, which it joins near the dorsal end of each secondary postgenal suture. The pretentoria are usually chitinized for the greater portion of their length. The metatentorina is also located at the bottom of a deep parademe, one of which arises on each side of the ventral portion of the margin of the foramen. These invaginations are always to be found just mesad of a large tendon which is supported by the parademe. The metatentoria are short and membranous and are located near the dorsal ends of the secondary postgenal sutures. The corpotentorium persists as a fine thread originating just caudo-mesad of the point where the pretentorium and metatentorium of each side join and extend across the ventral portion of the foramen between the metatentoria. In the more generalized families it is often thicker and sometimes heavily chitinized. It assumes the appearance of a delicate white thread in the Noctuidae. We are thus amply justified in concluding that the tentorium of lepidopterous larvae is very highly specialized, being not only vestigial, but also unusual in position and form.

Heavily chitinized parademes extend the entire length of the epicranial, fronto-clypeal and secondary postgenal sutures and along the dorsal and lateral portions of the margin of the foramen. The latter parademe is divided on each side by a short suture into a ventral and a dorsal occipital parademe. The ventral ones are the deepest of all of these infoldings, bearing the metatentorinae and the tendons already mentioned. They are the only ones not heavily chitinized. The fronto-clypeal parademe is not so well developed as the others. These secondary structures serve for support and for the attachment of muscles. They have been developed in correlation with the specialization by reduction which is characteristic of the tentorium of lepidopterous larvae.

The relative length of the epicranial stem presents more conspicuous variation than any other character in these larvae, except, of course, the number of uropods. In the majority of noctuid larvae the length of this suture is not strikingly different from that of the front. In certain Agrotinae, however, it is reduced to its adfrontal portion and in *Chamyris cerintha*, Erastrinae, it is markedly longer than the front, all gradations (Figs. 2, 15-17) between these extremes being found. The shortening of this suture, where it occurs, has been brought about apparently by a splitting apart of its two sides at the caudal end, the area between these separated sides being taken up by the coria continuous with the cervanotum. The triangular area thus formed is known as the vertical triangle, although morphologically it is composed of cervacoria and a part of the epicranial suture greatly widened. The apex of this triangle is usually heavily chitinized. The shortening of the epicranial stem is correlated with a general shortening of the cephalic aspect of the head, which has probably been induced by a change in the position of the head from the typical vertical one with the mouth-parts directed ventrad to a somewhat horizontal one with the mandibles directed cephalo-ventrad or cephalad in extreme cases.

The shape of the clypeus (Fig. 2) presents some variation, the frontoclypeal suture being either straight or curved upward in the middle more or less prominently. The relative widths of the preclypeus and postclypeus also vary to some extent. These characters appear to be of generic value. The width of the labrum relative to that of the clypeus and the depth of the labral cleft present characters applying to smaller groups. This sclerite is rarely nearly divided into two parts as in an undetermined species of Catocala.

The position of the ocellarae, although presenting no striking differences within the family, offers some convenient characters evidently applying chiefly to groups of species, although constant specific differences have been noticed in certain genera. In the majority of cases the distance between ocellarae 1 and 2 is distinctly less than that between 2 and 3, the line 1-2 often equalling one-half of the line 2-3. Sometimes 1 and 2 are nearly contiguous.

The coloration of the head is principally cuticular and, therefore, practically permanent in alcohol. Such markings offer much variation within the family, often providing easily recognizable specific characters. The general scheme of coloration is usually constant within a genus. In some species it differs markedly according to the instar. Individual variation is sometimes considerable. The entire head capsule is uniformly colored in but relatively few species. In these it ranges from light brown to nearly black according to the species. Often the vertex is darker than the rest of the head, the preclypeus especially being lightly pigmented. This

condition is widely distributed throughout the family. A peculiar reticulate fuscous marking is frequently found on the vertex, where it usually stands out prominently against the light brown background.

In 1896 Dyar introduced the first system for designating the setae of the lepidopterous larval head. He numbered those of each sclerite with Roman numerals from dorsal to ventral margin, departing from this scheme slightly on the ventral portion of the vertex. More recently Dampf has emphasized the taxonomic importance of the head setae in the Psychidae and their allies. He divided the head-setae into groups on the basis of the tendency exhibited to vary their position in the larvae of different species by groups rather than individually. This interpretation led him to refer to them according to these groups. In his study of microlepidopterous larvae Heinrich followed the system of Dampf, which he supplemented by numbering the setae, pointing out the fact that these group migrations are due to the contracting or expanding of the parts of the head-capsule. Fracker and Forbes designated the setae of the head by the Roman numerals of Dyar. Forbes also numbered the labral setae.

In devising a system which may be applicable to the study of the homologies of larval setae throughout the order, and very possibly throughout the larvae of different orders, it seems preferable to name them after the sclerites on which they occur rather than according to certain groupings which are not well understood, except perhaps in the few families studied by Dampf and Heinrich. The latter author disagrees with the former as to the group in which a certain seta should be included. It seems likely that in various families in which the trend of specialization has been divergent this grouping relation may be altogether different. We find in the Noctuidae, for example, certain setae within one of Dampf's groups exhibiting wide variation in position with reference to each other. The system of Dyar and Forbes, with minor changes, has, therefore, been followed in this paper.

These setae may be conveniently designated by the abbreviation for the sclerite bearing them followed by an Arabic numeral. Thus VI refers to the seta typically located furthest dorsad on the epicranium. The abbreviations, *o*, *v*, *a*, *f*, *c*, and *l* stand respectively for occiput, vertex, adfrontal, front, clypeus and labrum. A few minute setae hitherto disregarded, although of general occurrence, have been named. This same system of naming has been applied to the ocellarae, *oc* being the abbreviation used.

MOVABLE PARTS OF THE HEAD

The antennae of lepidopterous larvae appear to be generally uniform in structure and primary setal armature. That of *Cirphis unipuncta* (Figs. 19-21) may be regarded as typical for the order. The antennaria bears a

wide antacoria, which may be infolded or extended, permitting the antenna to be either protruded for its full length or retracted into the head so that only the distal portion is exposed. The first two segments are large, the third much smaller and the fourth very minute. These are separated by well developed coriae allowing free movement at the joints. The distal end of the second segment bears five primary setae of characteristic form, which may be named by combining Roman and Arabic numerals, the former referring to the segment, the latter to the seta. The seta III is the only one of these with a normal form; II 2 is extremely long and attenuate, being longer than the entire antenna; II 3, II 4, and II 5 are conical, II 4 being very minute. The distal end of the small third segment bears three conical setae, III 2 being midway in size between III 1 and III 3. A single attenuate seta is carried by the minute fourth segment.

Forbes has shown that the first three segments vary in relative size and that the proximal one sometimes bears secondary setae. The figures of Dampf and Tragardh are the only detailed ones of the antennae of caterpillars known to the author. The former investigator directs attention to the difference in the relative size of the conical setae in the Psychidae, where the condition is normal, and in the Talaeporiidae and the tineid *Adela degeerella*, where these setae are unusually large. Tragardh figures a most interesting series, representing the reduction of the antennae of leaf-miners. The minute size of the distal segment together with the great development of the third and its setae is apparently responsible for his failure to recognize this last segment as such, although it is distinctly shown in his figures. Most of the primary setae named can be identified even in these aberrant antennae. Packard's figures of the larval mouth-parts of Eriocephala appear to show four well developed segments, a unique condition for the order.

Within the Noctuidae there appears to be no variation in the antennae of taxonomic value, except perhaps the amount of chitinization. This varies from very slight to very heavy, the heavier chitinization being correlated with a darker color. The habit seems to bear no relation to the amount of chitinization, which varies according to the genus or sometimes within a genus.

The mandibles of caterpillars have been but little studied, accurate figures of them being scarce in literature. They are joined to the head immediately mesad of the antennae by a narrow mandacoria and to the lateral margin of the maxillae by a wide maxacoria. A large socket, the preartis, on the cephalo-dorsal corner serves for the articulation with the precoila and a large globose condyle, the postartis, on the opposite corner fits into the socket of the postcoila. A small caudal extensotendon and a large cephalic rectotendon provide attachment for the abductor and adductor muscles respectively. The left and right mandibles are usually unlike,

being formed so that the dentes of one fit into the emarginations of the other. Each mandible bears two large primary setae on its lateral aspect.

The great majority of caterpillars present no striking variation in the maxillae, although a few exceptional conditions have been recorded. Tragardh has discussed certain modifications found in those of the leaf-miners. Packard's figures of the larval mouth-parts of Eriocephala represent three free segments of the maxillary palpus instead of the two found in all families other than the Micropterygidae. Differences exist in the relative size of the segments in various families, as shown by the figures of Forbes. The noctuid larval maxilla (Figs. 24-25) is typical for the order, presenting the highly specialized condition found in that of all caterpillars.

The labium of lepidopterous larvae exhibits a degree of specialization unequalled even by the maxillae. The homologizing of its parts consequently presents a difficult problem. Its condition in the Noctuidae appears to be fairly typical for the order, although certain types of spinneret frequently occur within the family which are not generally found in caterpillars. The labium lies between the two maxillae, its proximal two-thirds being joined on each side to the cardo and stipes by a labacoria, which has been reduced in width to a mere suture. The submentum is large, as it is in the larvae of other orders, and is for the most part usually membranous or slightly chitinized. It is broadly attached to the ventral margin of the postgenae for the entire width of its proximal end by a narrow strip of membrane. This specialized condition has been brought about by the extension mesad of the postgenae, so that they separate the labium from the cervix, which typically bears this appendage in insects. The narrow strip of membrane which connects the postgenae and the submentum is evidently a portion of the cervacoria, which has become separated from the rest by the unusual development of these sclerites. The mesal portion of the submentum is occasionally not borne by the postgenae, since in many species they do not extend to the meson. A subtriangular sclerite located in each latero-proximal corner of the labium is of very frequent occurrence throughout the order and is apparently always present in the Noctuidae. Berlese does not figure these in his drawing of the mouth-parts of Acherontia, evidently considering them as secondary, if they occur in this species. Dampf refers to them as *postmentalstücke*, a term previously employed by Verhoeff, also regarding them as secondary, while Forbes, on the other hand, believed them to constitute the submentum, although they are not represented in several of his figures of the labia of caterpillars. The interpretation of the latter investigator leads him to consider as mentum the large membranous region regarded as submentum by Berlese, Dampf, and the author. The corresponding region in the coccinellid larvae is referred to as submentum by Gage and

that of the saw-fly larva figured by Berlese and Yuasa is so labeled. The absence of these sclerites in many lepidopterous larvae together with the fact that they are generally widely separated by the membrane and never constitute a single piece indicates that they represent merely two strongly chitinized areas of the submentum. They seem to have developed in correlation with the arms of the subcardines, whose chitinized portions lie adjacent to these plates of the submentum. The arms extend beneath the chitinized areas of the submentum and serve for the attachment of muscles, hence the advantage of these chitinous plates in the membrane adjacent to them. The membranous portion of the submentum always bears a pair of large setae.

The mentum is usually reduced or undifferentiated in specialized labia, the submentum being well developed and the stipulae always present. In caterpillars the mentum is not present as a distinct area, being presumably fused with the stipulae, which is the condition apparently found in all coleopterous, trichopterous, and saw-fly larvae. In those of the Lepidoptera the stipulae usually consist of a proximal chitinized ring and a distal membranous portion, which bears the palpigers and the vestigial glossae on which the spinneret is located. This area is referred to by Forbes but not named, whereas Berlese and Dampf consider it as the mentum. Just proximad of the proximal end of the spinneret on the caudal aspect there is a pair of minute setae.

The chitinized portion of the palpiger is typically an incomplete ring, its mesal and distal portions being membranous. Dampf has suggested that this structure may represent the basal segment of the palpus, in which case the palpiger must be regarded as undifferentiated. It varies much in width and shape throughout the order, resembling in Enocrania and Adela a basal segment of the palpus. In the Noctuidae it is not closely associated with this appendage, assuming the form of a semicircular sclerite lying in the membrane distad of a stipula. The mesal end of the caudal aspect of this semicircular sclerite is provided with two large sensoria. A reduction of the chitinized area mesad of the sensoria, which has frequently taken place throughout the order, has left them on the mesal end of the sclerite, where they remain surrounded partially or entirely by chitinized rings, the remnants of a more general chitinization. In the Noctuidae, where this reduction is usually marked, the distal sensorium is rarely completely surrounded, the ring being typically broken on its mesal side.

The two-segmented palpus has been correctly named by previous workers. The membrane which bears it within the semi-circular palpiger is generally wide, allowing free movement of this appendage. Its proximal segment is cylindrical, varying from stout to slender, the former shape being the most usual in the order and typical for the Noctuidae. It bears a terminal seta usually laterad of the distal segment, a minute cylinder

situated on the membranous end of the proximal segment. A terminal seta is also borne by the distal segment. These two setae are apparently of universal occurrence in caterpillars.

SPINNERET

The spinneret is located on the mesal portion of the membrane on the caudal aspect between the palpigers. The cephalic and lateral portions of its proximal end are surrounded by a semi-circular sclerite of varying width and shape, resembling the palpiger, although much smaller. A pair of sensoria are borne on the caudal aspect of this structure usually at its mesal ends. These sensoria are much smaller than those of the palpiger. A fold of membrane often extends distad from this sclerite surrounding the proximal end of the spinning organ, the tube through which the silk is extruded. This fold is usually much wider on the cephalic aspect, where it may assume the form of a long plate reaching nearly to the end of the spinning organ. Occasionally it is entirely chitinized, when it is indistinguishable from the proximal sclerite. The spinning organ varies extensively, presenting a great diversity of size, form, and modification. It ranges from entirely membranous to largely chitinized, from very long and tubular to short and flat. The silk-duct opens at its distal extremity.

Wide differences of opinion have been expressed as to the homology of this peculiar organ. A number of workers, represented by Packard, regard it as a modified hypopharynx, whereas Berlese and Dampf believe it to be formed of the fused glossae and paraglossae, the latter investigator even venturing to homologize the proximal sclerite and fold with the paraglossa and the spinning organ with the fused glossae. It seems very probable to the author, on the other hand, that this structure has developed secondarily. Those who regard it as hypopharynx appear to be misled by insufficient data. The silk-glands of lepidopterous larvae have reasonably been supposed to be the homologues of the salivary glands of the adults. Lucas subscribes to the same homology in the Trichoptera. The salivary glands of adult insects, so far as known to these investigators, opened at the base of the hypopharynx. Therefore, they reasoned, the silk-glands of caterpillars, which they regarded as the homologues of salivary glands generally, would presumably open on the hypopharynx, giving rise to the belief that this structure had been modified into a spinneret. MacGillivray has shown, however, that the salivary ducts of the Entopteraria open on the glossae of the labium, wherever these structures can be identified, and not at the base of the hypopharynx as in the Exopteraria, which was evidently the only condition known to these earlier workers. It seems questionable, therefore, whether these glands are homologous in the two superorders. However this may be, no evidence remains in support of the old view that

the spinneret has arisen from the hypopharynx, which, as will be shown later, is otherwise represented in lepidopterous larvae.

The position of the spinneret is that normally occupied by the glossae and paraglossae. It may represent the fusion of either or both of these lobes, altho its mesal position indicates that it is derived only from the glossae. Dampf's homologies, where he regards the paraglossae as represented by the proximal semicircle and the alaglossa by the spinning organ are, therefore, open to no serious objection by those who regard the spinneret as a primary structure.

Certain biological considerations lend weight to the view that the spinneret has developed secondarily, being without homologue in the typical insectean labium. Since the spinning habit appears in insects only in the larvae of Entopteraria, except in the Embiidae, where the glands open on the legs, it is evidently a secondary acquisition, which was not present in ancestral insect. The widespread occurrence of silk-spinning, however, in the larvae of Lepidoptera, Trichoptera, Hymenoptera, and Diptera seems to justify the conclusion that the common ancestral larva of these orders spun silk, although this habit has been lost in certain groups of each order, as Wheeler has shown it to be in certain families of ants. This acquisition has apparently developed furthest in the Lepidoptera, although it is possible that it was at one time equally extensive in the other orders mentioned, having been subsequently reduced. So far as known the spinneret is well developed only in caterpillars, the opening of the silkduct in silk-spinning hymenopterous, dipterous, and trichopterous larvae being without any well developed spinning organ and usually represented by a small aperture located near the distal end of the labium and surrounded by a chitinized ring. The glossae or paraglossae are rarely, if ever, well developed in these larvae. The condition of these structures leads us to suppose that they were probably vestigial in the ancestral larva of these orders, from which we may reasonably conclude that they are not well developed in caterpillars. The spinneret, therefore, is apparently a secondary development which evolved in correlation with the extensive spinning of silk. The proximal semicircular sclerite in lepidopterous larvae appears to correspond to the chitinized ring around the aperture in other orders and was apparently derived from the vestigial glossae. Although these conclusions are by no means certain, they seem to be the most reasonable on the basis of the evidence available.

The variations presented by the labium and their taxonomic value in the Noctuidae will now be considered. This appendage offers more extensive variation in caterpillars than any other structure, both in the form of its sclerites and of its distal lobes, especially of the spinneret, which exhibits the most diverse conditions. As Forbes has shown, the sclerites of the submentum present considerable differences in the extent of their

development. In the Noctuidae, however, they do not vary markedly, being typically as represented in *Cirphis unipuncta* (Fig. 24). The chitinized areas which occasionally appear in the membranous portion of the submentum in other families are rarely met with in the noctuids. The width and shape of the chitinized portion (Figs. 24, 28, 31) of the stipulae varies considerably according to the genus. Much generic and some specific variation is also presented by the chitinized portion (Figs. 26, 28, 31, 38, 44) of the palpiger. In the noctuids this sclerite exhibits a comparatively reduced condition and never appears as the basal segment of the palpus as it does in some other families. The long and slender type of palpus occurring in a few groups has not been found in the Noctuidae, this appendage exhibiting the stout form most common in the order. It varies, however, according to the genus or to larger groups in relative width and length and in the proportional size of the two segments. The setae of the palpus present differences within the family in form, size, and position. The one borne on the distal end of the proximal segment is usually located laterad of the minute distal segment throughout the order, although in certain noctuid genera it has migrated around the cephalic side of the distal end of the first segment until it appears mesad of the terminal segment, as in *Lycophotia margaritosa* (Fig. 38), a process revealed by postembryonic development. This is the only instance known to the author where a seta of the head or mouth-parts appears to have migrated by itself uninfluenced by movements of the cuticle. Forbes notes and figures an exceptional condition in an unnamed species of Catocala where there is apparently an extra small basal segment of the palpus. A similar development is often present in the Catocalinae due to the globular shape of the coria proximad of the basal segment. The situation figured by Forbes is evidently due to the secondary chitinization of this coria, the distal portion of the labium of this species exhibiting an unusual amount of chitin generally for a noctuid larva.

In spite of the very extensive variety of form offered by the spinneret, the amount of investigation which has been performed upon this interesting structure is surprisingly meager. Beyond Lyonet's figures showing the spinneret of *Cossus cossus*, those by Forbes of a species of Catocala and of *Thyridopteryx ephemeraeformis*, two by Dampf showing the mouth-parts of case-bearing larvae, and a short series of the labia of leaf-miners by Tragardh, there are no detailed representations of the spinneret known to the author. Yet this organ probably presents a greater range of variation than any other structure of lepidopterous larvae. The proximal semicircular sclerite varies much in width and shape, as Forbes has shown. It is typically broken on the caudal aspect, although its mesal ends (Fig. 31) are often joined by secondary chitinization, as in *Polia renigera*. This condition may exist in some groups as a primary one, since postembry-

ological evidence indicates that the semicircular sclerite was originally a complete ring, its reduction having begun on the meson and proceeded laterad. Its shape varies much within the family affording generic and specific characters. The proximal fold, which assumes a great variety of forms within the order, also exhibits marked differences within the family, ranging from membranous and rounded, the more usual condition, to chitinized, long and pointed, when it serves as a support (Fig. 32) for the spinning organ, which lies caudad of its caudal surface. This is the situation found by Dampf in the psychid genus Eumeta, which presumably led him to believe that this structure represents the paraglossae.

In three European species of Hepialus examined the spinneret is exceptionally long, tubular, and tapering, almost filiform, extending several times the length of the labial palpi. According to Packard it is well developed in Micropteryx, but his figures of the larval heads of Eriocephala, drawn from a few poorly mounted specimens, fail to show any spinneret. Most commonly throughout the order it is tubular, slightly tapering, truncate, and distinctly longer that the palpi. It is often supported (Fig. 32) by longitudinal chitinized areas, as in *Polia renigera*. In certain groups, notably the Sphingidae, Noctuidae, and Nepticulidae, it is short, flat, and stubby, frequently exhibiting a peculiar fringe (Figs. 26, 38, 39, 45, 46) in the two former families. When of this type in the Noctuidae the spinneret is often emarginate on the sides so that an upper and lower lip is formed, the latter usually being the longer. The lower lip may be deeply emarginate, as in *Cirphis unipuncta* (Fig. 27) or bilobed, as in many Agrotinae. Both lips or the upper one only may be fringed. All stages in the development of the fringe are represented by various species of noctuid larvae. It appears to have developed on the upper lip earliest in phylogeny (Figs. 45, 46) appearing later (Figs. 26, 39) on both surfaces.

With the exception of the subfiliform type of Hepialus, all forms of spinning organ observed in other families are represented within the Noctuidae, this family probably presenting a greater range of variation in its spinneret than any other. In the Agrotinae it is often much shorter than the palpi, flat, with upper and lower lips, and frequently bilobed or fringed, or it may be long and pointed, as in Chloridea. It ranges from long and slender to fairly stout and about equal to the palpi in length in the Hadeninae, being either truncate and fringed, as in *Cirphis unipuncta*, or pointed, as in *Moliana albilinea*. Most commonly it is distinctly longer than the palpi in this subfamily and is apparently never markedly shorter, as it is in the Agrotinae. In the species of Cucullinae, Phytometrinae, and Hypeninae examined it is much longer than the palpi and usually tapering. It distinctly exceeds the palpi in length in the Catocalinae, where it ranges from stout to slender. The spinneret of the Acronyctinae varies from slightly to greatly longer than the palpi, presenting an extensive variety of

form. Larger groups of genera or even single genera may be often separated by characters based on the length and form of the spinneret more readily than by any other means. The general type of this organ is usually the same for large groups. Some of the most fundamental and valuable characters for the taxonomic treatment of noctuid larvae are provided by the spinneret. The failure of previous workers to appreciate the phylogenetic significance of its variations has probably been due to its small size, which often necessitates the removal of the labium to allow careful examination. This operation, however, is performed with the utmost readiness by means of a single stroke of a needle.

The types of spinneret within the Noctuidae, unlike those of the mandibles, can be largely correlated with biological characteristics. The amount of silk employed as a protective covering for the pupa varies extensively according to the situation in which pupation takes place, the type of location selected being generally characteristic for the taxonomic group. Noctuid larvae usually pupate either within a cocoon or a subterranean cell. The cocoon may be fairly dense, as in many Acronyctinae and Phytometrinae, to very slight, as in the genus Polia of the Hadeninae. It never approaches those of the Saturniidae in density or in the amount of silk employed, being usually very slight, although often supplemented by foreign matter such as leaves or grass or by setae from the verrucae in Acronycta, where these structures are present. Those which pupate beneath the soil, on the other hand, usually spin but a few threads, as in *Cirphis unipuncta*, or no silk whatever, a condition exemplified by most species of Agrotinae which have been reared by the author.

This reduction in the amount of silk used for a pupal covering is also met with in certain other families, notably in the butterflies, where only a button of silk is spun for the attachment of the cremaster, in the Sphingidae, which usually enter the soil to pupate, spinning little or no silk, and in certain leaf-miners, which, according to Trägardh, have lost this habit in correlation with their protected habitat. The accompaniment of pupation beneath the soil or in similarly protected situations by a marked reduction in the amount of silken covering, appears to be of general if not of universal occurrence. It should be noted, however, that the converse is not true, the naked pupae of butterflies having developed other means of protection than subterranean pupation.

An interesting instance of individual variation in the amount of silk spun is furnished by four larvae of *Polia lorea*. Two were taken on the floor of typical Illinois forest, the other two being collected on the following day on the prairie, about six miles from the nearest woodland. The latter were feeding upon sweet clover, the former upon some plant not definitely known, probably *Geranium maculatum*, but not upon any species of Trifolium, since none was present in the vicinity. The two larvae of the

prairie spun fairly dense cocoons, while a mere network of threads covered the pupae of the individuals collected in the forest. All four pupated on the surface of the ground among grass on the same day under approximately the same external conditions. Since both sexes were represented by those of the prairie, the difference in the amount of silk spun was not a sexual one. A question of considerable interest arises as to whether this striking biological variation is to be explained by the direct effect of different food upon the activity of the silk-glands or upon the basis of physiological adjustment to environment, the pupae of the prairie requiring more protection from the sun than those of the forest. Instances of much less pronounced individual variation in this respect have been frequently noted with various species reared.

Contrary to what would perhaps be the natural supposition, the subterranean mode of life frequently exhibited by noctuid larvae, exemplified by the cut-worms, appears to bear no definite relation to the habit of pupation beneath the soil. Larvae which never enter the earth during the feeding period often pupate in earthen cells, while some species showing pronounced subterranean tendencies as larvae always spin slight cocoons among the debris on the surface of the ground. Similarly the Sphingidae, which usually undergo pupation in the earth, are never subterranean as larvae so far as known. The habit of pupation in the soil is a fundamental one which remains constant throughout large groups, whereas the degree of development of the subterranean mode of life in larvae is variable in closely related species.

Caterpillars which spin much silk are generally provided with a long, slender, tubular, tapering spinneret. The short depressed type is apparently found only in those groups whose larvae spin little or no pupal covering. The Sphingidae and Noctuidae which pupate in earthen cells and certain leaf-miners which undergo this process in their mines without spinning silk present this reduced type of spinneret. It has not been found to occur where the spinning habit is well developed. The general accompaniment in the Noctuidae of the short flat spinning organ by the marked reduction or entire loss of silk-spinning is unquestionable. Some species with the long type of spinneret, however, pupate in the soil, as instanced by *Chloridea armigera*. This condition is to be expected in those species whose last instars spin silk during the feeding period. *Sidemia devastatrix* has been observed by the author to spin a cocoon in which to undergo ecdysis, a peculiar habit, which, so far as known, has not been recorded for any other caterpillar, except for certain leaf-miners studied by Trägardh.

The peculiar fringe borne on the distal end of the spinneret has been found only in noctuid and sphingid larvae with subterranean pupae. Although the function of this strange modification has not been definitely determined it seems probable that it is used as a brush to distribute a

secretion of the silk-glands over the inner surface of the earthen cell. Examination of the inside of these cells seems to reveal the presence of such a substance. This lining serves perhaps to render the cell waterproof or to prevent it from crumbling. The burrows leading to the pupal cell of *Chloridea armigera* have been observed to be fortified with a similar secretion of unknown origin, although the spinneret of this species bears no fringe. Chapman observed that the thread spun by the flat short spinneret of the earlier instars of the leaf-miner, *Limacodes testudo*, assumed the form, not of a thread but of "a very thin ribbon," indicating that the semifluid silk may issue from the spinneret in different physical states. A microscopic study of the silk of noctuid larvae, as well as an investigation of the comparative morphology of the silk-press promises to throw light upon this question.

Both morphological and biological evidence indicates that the long cylindrical spinneret represents the ancestral condition for the Noctuidae. The development of this type to a very marked degree in Hepialus, the well developed spinneret in Micropteryx, and the general occurrence of the long spinning-organ throughout all caterpillars seem to justify this conclusion. As previously stated, the widespread distribution of the silk-spinning habit throughout trichopterous, hymenopterous, and lepidopterous larvae and its appearance in those of certain dipterous families indicates its development at an early phylogenetic period. Its absence or reduction in members of these orders may reasonably be regarded as a specialization. Since the loss or reduction of this habit in noctuid larvae, which is evidently a biological departure from the ancestral condition, is generally correlated with the short, flat spinneret, we must conclude that this type of spinning-organ is a specialized one derived from the tubular type in correlation with subterranean pupation.

PREPHARYNX

The hypopharynx of caterpillars has been largely neglected, the sole morphological studies of this structure having been performed by Trägardh on the leaf-miners, where it frequently presents a highly modified condition, and by DeGryse, who has written a brief paper on this subject, embracing a number of families. The only detailed figures of the normal hypopharynx of lepidopterous larvae known to the author are those by Dampf of two species of case-bearing caterpillars, and a few by DeGryse. It assumes the form of a large membranous lobe lying cephalad of the labium and continuous with it, and extends dorsad as a rather low mound forming the lower floor of the prepharynx. A narrow sclerite continuous with the chitinized portion of the stipula extends longitudinally on each side of its proximal end, corresponding apparently to the lingula shown by Yuasa. In many noctuid larvae the hypopharynx is distinctly divided into

a ventral portion, which follows the general contour of the labium, and a dorsal mound-like part, which resembles the subgusta in the Orthoptera (Fig. 25). Very often this division is not clearly marked, as in Dampf's figure of the psychid Eumeta and in the noctuid *Lycophotia margaritosa*. The question as to whether it is primary or secondary cannot be decided upon the basis of our meager knowledge of the condition, generally found within the order. It is very possible that the dorsal portion may be homologous with the subgusta of the Orthoptera, although the entire structure may represent the hypopharynx, in which case the division must be regarded as secondary.

The hypopharynx typically bears numerous small setae, whose distribution, form, size and number vary greatly within the family, offering excellent generic and specific characters. They are rarely apparently absent, as in Rhodophora and Xylina or may, on the other hand, cover the entire distal portion of the hypopharynx. Frequently the pubescence does not begin immediately cephalad of the labial palpi, leaving a glabrous area in this region, as in Monima, Epizeuxis, and Platyhypena. The setae may be approximately equal in length, as in *Lycophotia margaritosa* or longer toward the postpharynx, as in Nephalodes, or shorter in this region than the setae near the labium, as in *Sidemia devastatrix*. In Phytometra and Chloridea they are longer on the sides of the hypopharynx than in the middle. They may be sparse, as in Platyhypena, but are more often very densely distributed. They vary greatly in length, sometimes attaining that of the palpi, as in *Cirphis unipuncta* (Fig. 26), but are most frequently much shorter, like those of *Lycophotia margaritosa* (Fig. 38), or stout and very minute as in *Agrotis ypsilon* (Fig. 44). In *Lycophotia infecta* they are so short that the surface of the membrane appears granular. No correlation between these various conditions and the feeding habit has been discovered. The function of these setae is probably essentially protective, although they may serve as sensory organs.

The epipharynx of lepidopterous larvae is membranous and continuous with the labium on its ventral and lateral margins and with the postpharynx at its dorsal end (Fig. 13). It bears a pair of narrow longitudinal sclerites, the tormae, which lie entad of the ends of the clypeo-labral suture. Three stout primary setae are borne on each side in the membrane near the ventral margin. A fourth minute seta figured by Dampf in the psychid genus Eumeta has not been found in the Noctuidae. No modifications of the epipharynx, such as those which occur in the leaf-miners, have been encountered in the family. Neither the form of the torma nor the position of the setae is subject to marked variations.

SETAE OF TRUNK

A number of the earlier students of lepidopterous larvae noted the definite arrangement of certain setae throughout large groups, which led them to investigate the taxonomic value of setal position. Müller in 1886 and Dyar in 1894 published important works on this subject, the latter attempting to make a table to the families of Lepidoptera based on the setal pattern of the larvae. The distinction between primary and secondary setae was recognized by Müller, Dyar subsequently introducing the term subprimary, which he applied to setae of general occurrence which are absent from the first instar. The most extensive researches on the setae of the trunk have been performed recently by Fracker in 1914 and by Schierbeek in 1917. The former author has provided us with a most useful and easily workable table for the identification of caterpillars, exclusive of the Noctuidae, in which work the setae play an important part. The latter investigator pursued the subject from the morphological point of view rather than from the systematic one. These two workers disagree on the selection of a primitive type of setal position, Fracker regarding the prothorax as presenting the more generalized position, while Schierbeek gives good reasons for considering the abdominal segments which bear larvapods as the more primitive. They hold different views, moreover, as to the homodynamies between thoracic and abdominal setae. On at least one important point they agree, namely, that verrucae correspond to single primary setae, the former having been developed from the latter, and, in certain groups, having been subsequently reduced again to single setae, this process being a reversible one.

Inasmuch as an investigation purposing to settle the disagreements of these two workers would involve a detailed study of the larvae of the whole order, the disputed questions of homodynamy and primitive segments cannot be decided from researches on the Noctuidae alone. It is consequently not a part of the plan of this work to discuss these points. The treatment of the setae of the trunk here presented will be confined chiefly to a discussion of the variation in the setal pattern of noctuid larvae, exclusive of those which bear verrucae, as in Acronycta. The forms with tufts of setae are confined within the family to this genus and to a few allied ones of little importance. Since they present various stages in the development and reduction of verrucae, these genera promise a rich field for the study of the evolution of setal tufts.

Of the various systems of naming setae which have been proposed that of Fracker is undoubtedly the most satisfactory. As Schierbeek states, the older system of numbering them has resulted in so much confusion that any further schemes employing numerals would only increase our difficulties. He rejects Fracker's Greek letter system, apparently because he disagrees with the homodynamies proposed by this author, and proceeds to apply

names descriptive of the location of the setae to which they refer. We fail to understand why a difference of opinion as to homodynamy should render advisable the addition of yet a new system to our already superfluous supply. The fact, moreover, that particular setae may be located in widely different positions according to the segment and to the species opens to objection all names of setae descriptive of position. Schierbeek would change the names of the setae in instances of this sort, maintaining a nomenclature should provide a simple means of describing larvae, rather than of indicating questionable homologies. Inasmuch as the general progress of all morphology and of taxonomy, which should always be based on morphology, depends largely upon the correct homologizing of structures, we can by no means accept this view, even in cases where the homologies indicated by the nomenclature are doubtful. The shortness of the names of Greek letters compared to the very long ones proposed by Schierbeek also favors the use of the former. Furthermore, because of the great utilitarian value of Fracker's tables, this system will probably come into more general use than any other. For these reasons it will be used in this paper so far as possible. Schierbeek's plan of naming the types of setal arrangement of numerals seems very commendable. No occasion arises, however, for using it in this work.

Except for the marked differences in the development of verrucae exhibited solely within a few genera of the Acronyctinae, the setae of noctuid larvae offer comparatively little variation. Certain minor variations in their number and situation, however, are of great phylogenetic significance because of their fundamental nature. Figures 47, 48, and 49, showing the setal position in *Cirphis unipuncta*, represent the typical condition for the family. The naming of the setae in these figures differs slightly from Fracker's labeling of those of *Feltia gladiaria*. As clearly shown, both by his own figures and by those of the author, his tau on segments 7 and 8 should be omega. The setae on the anal larvapod are not named in his figure of Feltia, where their number and position is quite different from that in Hepialus. Consequently the letters used to designate these setae may not correspond to those in Fracker's figure of Hepialus, which, as he states, do not necessarily indicate homodynamy with setae bearing the same names on other segments. The seta on the anal segment of Feltia which apparently corresponds to his theta on Hepialus is primary in the former, since it occurs in the first instar of this species. Consequently it should not be called theta, which is subprimary according to Fracker. It is referred to as kappa in this paper.

Certain minute setae are omitted from Fracker's figure of Feltia. Omega should be present on segments 1 and 9 and the minute setae labeled x in our figures were either generally overlooked by him or considered as secondary. These seem to have escaped the notice of all workers but Forbes

and Dampf in spite of their widespread occurrence in the order. The latter figures them in the psychid, Eumeta, and the former in an unnamed noctuid and in Incurvaria, where he labels them xa, xb, xc and xd. They have been found by the author in nearly all noctuids examined and in the cossid *Zeuzera pyrina*, where they are extremely minute. They are undoubtedly primary, since they have been seen in the first instar of *Cirphis unipuncta* and of *Phytometra brassicae*. They most probably occur in all newly hatched noctuid larvae, if not in those of all caterpillars. Their extreme minuteness renders necessary a most careful search in order to locate them. The ventral two, xc and xd, occur only on the mesothorax and metathorax and apparently correspond to the subprimary gamma of Fracker, which, he states, is primary on the prothorax. These setae perhaps represent a vestigeal verruca, the two together being homologous with one seta. In Hepialus there are three small setae in this region instead of two, as Fracker has shown. On the Noctuidae either one or both of the minute setae xa and xb are present on all segments but the prothorax and the anal one. Xa of the mesothorax has apparently migrated onto the caudal margin of the prothorax. These two setae appear to represent but one primary one just as a verruca corresponds to a single seta.

The homodynamy of these four minute setae cannot be definitely established without involving an extensive study of the setal patterns of caterpillars in general, especially of the first instars. Their position, nevertheless, suggests homodynamy between alpha of the prothorax and xa plus xb of the following segments and between gamma of the former and xc plus xd of the mesothorax and metathorax. If this be true, beta and delta of the prothorax correspond respectively to alpha and beta of the following segments, other homodynamies remaining unchanged. This interpretation reveals a much closer similarity between the prothorax and other segments than that of Fracker, in which the minute setae were disregarded. It seems preferable, however, to retain the names of Forbes for these setae pending more extensive study on this question.

Variations in the setal pattern of the prothorax are clearly discernible and generally fairly constant for genera but they are so slight and grade so continuously that very little taxonomic aid is afforded by them. The location of beta varies longitudinally to some extent, ranging from a position on the transverse line of beta to one distinctly caudad of it. Rho exhibits some transverse variation, being either equidistant from delta and the spiracle, as in *Polia meditata*, or much nearer to the latter, as in *Nephelodes emmedonia*. The situation of epsilon with reference to gamma and to the spiracle offers the best character in setal position on the prothorax. In the Acronyctinae, Cucullinae, and Hadeninae epsilon may be distinctly nearer to either according to the genus. It is apparently always nearer to the spiracle on the Catocalinae and Phytometrinae, but ranges in the

Agrotinae from a point equidistant to one much nearer to gamma. Epsilon also varies in position in the Hypeninae, being equidistant from gamma and the spiracle in some genera and nearer to the spiracle in others. Some longitudinal variation is offered by epsilon, which may be slightly or considerably caudad of kappa according to the genus. Kappa varies slightly but quite constantly in transverse location, ranging from a point distinctly above the spiracle to one a little below it. The relative situation of eta, kappa and the spiracle with reference to one another differs according to the group. Eta is usually distinctly below kappa and slightly caudad of it, being much nearer to kappa than to the spiracle. These setae may, however, be on the same longitudinal line, with kappa so far caudad that it is equidistant from eta and the spiracle.

As in caterpillars generally the mesothorax and metathorax are very similar to each other, although they exhibit a quite different setal pattern than the prothorax, the arrangement on the former segments resembling rather closely that of the abdominal ones. The mesothorax and metathorax differ from those which follow chiefly in the longitudinal position of alpha and beta and in the situation of the setae occupying the region which bears the spiracle in other segments. One or both of the minute setae xa and xb may be present on the mesothorax, this point representing individual variation. Both are usually present on the metathorax. On the mesothorax beta varies from a position on the transverse line through alpha to one distinctly cephalad of it. The location of beta may be the same on the metathorax as on the mesothorax or it may, as is often the case, be a little further caudad on the metathorax (Fig. 48), the amount of variation in this respect remaining the same for both segments. On both mesothorax and metathorax rho varies longitudinally from a point distinctly cephalad to one a little caudad of epsilon, the latter condition being commonly found in the Agrotinae. A greater difference in position is presented by beta, which on the mesothorax may be either equidistant from alpha and epsilon or very much nearer to alpha as in Catocala. On the metathorax beta is usually further ventrad, varying the same amount as on the mesothorax. The position of a line drawn through rho and epsilon with reference to kappa and theta furnishes one of the best characters on these two segments. The condition in this respect is usually the same on these segments, but may be distinctly different as in *Achatodes zeae*, showing that there has been some independent variation in the setal position, notwithstanding their very similar organization. In the Agrotinae and Catocalinae examined this line passes nearer to theta than to kappa. It may be distinctly nearer to either one in the Hadeninae, Acronyctinae and Hypeninae according to the genus. In the Phytometrinae it is usually equidistant from the two setae and ranges from a point equidistant to one much nearer to theta in the Cucullinae. The situation of

kappa, theta, and eta relative to one another also varies sufficiently to provide some characters. Kappa may be equidistant from eta and theta or very much nearer to eta. Most commonly it is slightly but distinctly nearer to the latter, being especially close to theta in the Catocalinae, Phytometrinae, and Hypeninae, a group of subfamilies which, as will be shown later, conform as a unit to certain other very fundamental characters. The angle made at kappa by the lines kappa-eta and kappa-theta varies in size from 80 degrees to a very obtuse one according to the genus. The most marked variation in setal position exhibited on the mesothorax and metathorax is furnished by xc and xd. Although closely associated, they vary not only relative to each other but also in transverse position with reference to epsilon and rho, ranging from a point a little above rho to one slightly below epsilon, the latter condition having been found only in *Achatodes zeae*. Their minute size, however, would render impractical their use in tables. The fact that much greater variation occurs in the setal arrangement of these segments than in the prothorax would seem to support Fracker's contention that the condition in this respect is more primitive in the latter. The setal pattern of the mesothorax and metathorax, however, is on the whole very uniform.

The arrangement of the setae of abdominal segments 1 and 2 differs essentially from that of the other segments only in the region where larvapods are borne on the following segments. The setae which are normally borne on the larvapods on segments 3, 4, 5, and 6 are present on this portion of segments 1 and 2. The other setae of these two segments will be considered later in the general treatment of the abdominal setae which follows. On segment 2 tau is apparently always well developed, but it has been found on segment 1 only in the Catocallinae, Phytometrinae and Hypeninae. Fracker figures it in the first abdominal segment of *Feltia gladiaria*, although the author has failed to find it in an abundant supply of material of this species. Omega, on the other hand, which is omitted from his figure, is apparently always present in the family on this segment, although very minute. The presence or absence of tau is the most fundamental character discovered in our entire study of the morphology of the noctuid larvae, making it possible apparently to separate two large groups of subfamilies on this basis. The position of omega varies considerably in a transverse direction according to the genus, its minute size, however, renders it inadvisable to use this variation in tables. Some difference in longitudinal location is offered by sigma, which ranges from a position on the transverse line through pi to one distinctly caudad of it. The Catocalinae apparently differ from other subfamilies in having the line nu-mu longer than the line pi-mu on segments 1 and 2, the opposite condition being distinctly present in all other larvae examined. On both these segments, in those subfamilies where it occurs, tau varies both longi-

tudinally and transversely, furnishing good generic characters throughout the family. It may be nearer to pi or to sigma and varies from a point on the transverse line through nu to one just cephalad of the transverse line through pi.

Only one of the minute setae xa and xb is usually present on the abdominal segments, altho both are found in *Chloridea armigera* and frequently the persisting seta is associated with a minute spot, which evidently represents the vestige of the other. The transverse variation in the location of xa with reference to alpha and beta affords some phylogenetic indications, altho the minute size of xa precludes the use of its variations in tables. Typically this seta is further dorsad of beta on segment 1 than on segments 2 to 7 inclusive, being most ventrad of all on segment 8. This variation involves the migration of beta as much as that of xa. Two genera examined, Catocala and Xylina, afford exceptions to the rule, xa being further dorsad relative to beta on segment 8 than on 1. In all other groups investigated xa is ventrad of the longitudinal line through beta, whereas in these two genera it is much dorsad of this line, an instance of parallel development.

The difference in the longitudinal position of the spiracle with reference to the surrounding setae on successive segments in the individual follows a certain definite plan throughout the family. On segment 1 the transverse line through rho ranges according to the group from a position distinctly cephalad to one a little caudad of the spiracle. Rho is clearly further cephalad in segments 2 to 6 inclusive than in 1, its transverse line passing cephalad of the spiracle or tangent to the cephalic margin. Segment 7 presents approximately the condition found in segment 1, the seta being further caudad than in segments 2 to 6, and ranging from a situation cephalad of the spiracle to one caudad of it. Two exceptions to this general plan have been noted. In *Sidemia devastatrix* the condition on segments 1 and 7 does not differ clearly from that in the intermediate segments and in *Papaipema nebris* segment 7 exhibits the same location which it occupies on segments 2 to 6, segment 1 differing from the rest as usual. The fact that segments 1 and 7 show much greater variation in this respect than the intermediate segments indicates that the condition found on segments 2 to 6 is the more primitive. Evidently in segments 1 and 7 the spiracle has migrated cephalad of its primitive position. In some cases this process has proceeded further on segment 1 and with other species on segment 7. The condition on segment 8, where the position of rho varies according to the group from a location cephalad to one caudad of the spiracle, reveals no uniform relation to that on other segments. Altho these minor variations in the longitudinal situation of the spiracle offer points of morphological interest they usually do not lend themselves readily to taxonomic application. The Catocalinae, however, apparently differ from all other groups within the family in having rho distinctly cephalad of the spiracle in segment 1.

The spiracle has also migrated in a transverse direction, as indicated by its position with reference to the surrounding setae. In general it is further ventrad on segment 1 and further dorsad on segment 8 than on segments 2 to 7 inclusive. Sometimes segments 7 and 8 present the same condition, as in *Scolecocampa liburna*, which is to be regarded as a specialization, since segment 7 as well as segment 8 has departed from the primitive arrangement. In Sidemia segment 8 does not differ in the transverse position of the spiracle with reference to epsilon from segments 2 to 7, as it does in the other genera examined. This may be reasonably considered as a generalization.

From this consideration of the position of the spiracle it appears that segments 2 to 6 inclusive present the primitive condition, the spiracle having migrated cephalad on segments 1 and 7 and either cephalad or caudad on segment 8 depending on the group. It has, moreover, shifted ventrad on segment 1 and dorsad on segment 8, remaining usually in the same transverse position on segment 7 as on segments 2 to 6.

The taxonomic value of the transverse variation of kappa in caterpillars was early demonstrated by Dyar. Altho the situation of this seta offers no conspicuous differences in this family, it varies sufficiently to provide some generic characters. It is usually much further ventrad of the spiracle on segment 7 than on other segments. *Achatodes zeae* again affords an exception, having kappa further ventrad on segment 8 than on segment 7, the reverse usually being true. Differences in the location of eta and mu afford generic characters, especially on segment 7, where they vary both transversely and longitudinally. The transverse position of omega relative to pi and sigma varies considerably throughout the family, seemingly according to the genus. The very minute size of omega, however, unfortunately precludes the use of this character in a table.

On segment 8 beta is typically much further dorsad than on the segments cephalad of it, presenting a specialized setal arrangement. The longitudinal line through alpha may pass considerably above beta or a little below it, the latter more specialized condition being less frequently encountered. This character promises to be useful in the separation of genera and of larger groups. Pi varies transversely to some extent on segment 8 relative to mu and sigma, affording generic characters.

With the exception of the anal one, segment 9 may reasonably be regarded as the most specialized segment with respect to setal pattern. Here the migration dorsad of beta has proceeded much further than on segment 8. The transverse location of alpha relative to beta and rho varies according to the group, altho presenting considerable individual variation in some species. Rho may be nearer either to alpha or to beta depending on the genus. The transverse line through kappa may pass either caudad or cephalad of pi, both of these setae varying somewhat in their situation

according to the group, altho they provide no convenient characters for use in tables.

The setae of the anal segment, which probably represents the fused tenth and eleventh abdominal somites, cannot be definitely homodynamized with those of other segments. Alpha, beta, and kappa vary a little in relative position according to the genus or in some instances within a genus. Kappa is most commonly equidistant from the other two but may be distinctly nearer to beta or less often slightly nearer to alpha. Both extremes have been found within the genus Phytometra. The position of the setae on the lateral aspect of the anal larvapod is perhaps subject to more striking variation than any other group of setae on the trunk of noctuid larvae. An usually conspicuous sensorium, which McIndoo has described, also contributes to the taxonomic value of this region, varying considerably in situation relative to the setae. Eta may be nearer either to epsilon or to omega, furnishing a basis for the separation of genera and larger groups, altho occasionally showing specific variation. *Scolecocampa liburna* presents an exceptional position of the sensorium, which is distad of eta (Fig. 53). In all other species examined it is distinctly proximad of the setae. The sensorium, eta, mu, and tau are frequently arranged so as to form the points of a diamond, which varies considerably in relative length and width, according to larger groups. The line from the sensorium to tau is usually longer than the one from mu to eta, altho the reverse situation is sometimes encountered. Either mu or eta may be nearer to the sensorium, so that the diamond is often out of true. Mu varies in location with reference to the lines epsilon-eta and omega-tau, being nearer to either one. All of these variations appear to apply chiefly to genera.

LARVAPODS

The general form of the larvapods of noctuid larvae (Figs. 50-53) is typical for the entire order. As in a number of related families, the crochets are arranged in a mesoseries and are homoideous and uniordinal (Figs. 51, 58) representing a supposedly specialized type which Dyar considered to have descended from the circular one found in Hepialus. They are operated by muscles which attach entad of a small usually heavily chitinized spot in the center of the distal end of the uropod. As shown in Figure 59 each crochet lies within a membranous invagination whose mesal edge bears a number of pointed membranous projections. These have not been previously described, so far as known. Their function is problematical. The proximal end of each crochet is pointed and curved mesad, serving for the attachment of muscles. Since the larvapods represent embryonic abdominal appendages which have persisted into postembryonic life, the terms proleg and false leg in general use are inappropriate.

Altho the extent of variation in the larvapods of noctuids does not approach that which Goosen's series of these appendages reveals in the entire order, they differ quite markedly in form, number, relative size, number of crochets, and amount of chitinization. The setal arrangement is practically uniform. As previously stated, from two to four pairs of median larvapods may be present, the first one or two pairs, which are located on the third and fourth abdominal segments, being absent in certain groups. In the Phytometrinae the two cephalic pairs are usually wanting, altho Hampson mentions one genus whose larvae have the full number. The Catocalinae exhibit a pronounced tendency toward the reduction of the first two pairs, which reaches its acme in Caenurgia, where they are entirely absent. The first pair only are generally lacking or without crochets in the Hypeninae. According to Hampson, the Erastrinae also bear but three pairs of median larvapods, altho the larva of *Chamyris cerintha*, which was evidently unknown to him, has the full number, the first pair being as well developed as the rest. The larvae of other subfamilies of which material has been available for study are provided with four pairs of median larvapods with the first two pairs usually not strikingly smaller than the others. In certain Phytometrinae the vestiges of the lost larvapods can be discerned as heavily chitinized small protuberances bearing the setae in about the same position which they occupy in the fully developed appendage. *Epizeuxis lubricalis* of the Hypeninae has the first pair fairly well developed but completely lacking crochets. The number and relative size of the larvapods furnish very fundamental characters, altho no noctuid subfamilies can be reliably diagnosed upon this basis alone.

Since the caterpillars of the most generalized families and of the great majority of all Lepidoptera bear four well developed pairs of median larvapods, this is most reasonably regarded as the generalized condition. Their reduction has taken place in a few very distantly related groups, this process having proceeded to a different extent in each. In the Cochlidiidae they are entirely absent and in the Geometridae only the last pair of median ones and those of the anal segment persist. Certain groups of Noctuidae, apparently represent an incipient stage in this process of reduction, as exemplified by the Agrotinae, in which the first two pairs are typically somewhat smaller than the rest. In the Catocalinae the same tendency is exhibited to a much greater degree. The Phytometrinae and Hypeninae, whose larvae are generally the most highly specialized in the family in this respect, are placed by Hampson among the most specialized noctuids on the basis of the structure of the adults, whereas the larvae of the Acronyctinae, which he regards as a relatively generalized subfamily, always have the full number of larvapods well developed.

There appears to be no very definite correlation within the family between the mode of life and the loss or reduction of the first two pairs of larvapods, although this condition is accompanied by the habit of walking with a looping gait and of moving more rapidly, a point to be discussed in connection with the postembryology of the larvapods. The lengthening, however, of the two latter pairs of median and of the anal ones, which is so pronounced in larvae of Catocala, appears to be a modification for arboreal life. The same specialization is found to a lesser degree in many arboreal caterpillars. This type of larvapod seems to be found only in larvae that climb extensively. The fact that the development of this modification has proceeded further in the catocalas than in most other arboreal larvae is consistent with the occurrence in this genus of a number of marked adaptations to life in the tree stratum of the deciduous forest. The eggs, larvae, and adults are protectively colored like the bark of the trees on which they rest. Practically all of the species feed upon the foliage of deciduous trees or upon plants of the deciduous forest.

The number of crochets is larger in Catocala than in most noctuid larvae, which is apparently a further specialization for climbing on the trunks and twigs of trees. From the first to the anal pair of larvapods respectively the number of crochets in *Catocala grynea* is 30, 36, 43, 55. The other extreme is presented by some of the subterranean forms, *Feltia gladiaria* having 8, 12, 14, 14, 18 and *Sidemia devastatrix* 12, 14, 14, 14, 14. In general the anal pair has the largest number and the first pair often bears a few less than the others. The formula for *Cirphis phragmitidicola*, 22, 24, 26, 30, represents an average one for the family. Some individual variation occurs in this respect, the number varying two or three each way from the mean. It is frequently different on the two sides of the same individual, as Dampf has shown it to be in the psychid, Eumeta. Considerable difference in the number of crochets is sometimes exhibited by closely related species, *Polia meditata* having 16, 18, 18, 20, 26, and *renigera* 12, 12, 16, 18, 19. These two species are decidedly subterranean. The closely related *Ceramica picta*, on the other hand, which enters the soil only to pupate, frequently climbing shrubbery to feed, has 26, 27, 30, 32, 35. Beyond the presence of a larger number in the arboreal forms, there appears to be no marked correlation between the mode of life and the number of crochets, altho the smallest number is apparently best represented among species which burrow in the soil. Specific determinations may often be facilitated by these formulae, altho a considerable difference in this respect according to the instar necessitates a positive knowledge of the stadium before applying this character.

POSTEMBRYOLOGY

Ecdysis is undergone by noctuid larvae four, five, or six times, depending chiefly on the species, but somewhat on other factors. They present, then, five, six, or seven stadia. After each molt the postembryonic changes which have taken place during the previous stadium are suddenly revealed. These changes may be highly conspicuous, but are more often so very slight that careful observation or accurate measurement is necessary to detect them. Before considering the structural changes undergone in larval postembryology, we shall discuss at this point the significance of the number of stadia, and of the amount of increase in size from one stage to the next.

NUMBER OF MOLTS

Although not absolutely fixed, the number of molts characteristic for species of lepidopterous larvae is not subject to the considerable variation found in some other orders. Wodsedalek, for example, greatly increased the number of stadia in the larvae of Trogoderma (Dermestidae) by starvation. It is certain that environmental factors may at times cause one molt more or less in certain lepidopterous larvae. Payne found that those of *Ceramica picta* pass but five stadia in both generations in Nova Scotia, whereas those reared in Illinois by the author have uniformly undergone one molt more than these northern individuals. Hibernating butterfly larvae have been known to molt once more than those of the summer broods. This phenomenon has not been found in the noctuid larvae, *Agrotis c-nigrum* and *Polia renigera*, which have been reared through both winter and summer broods. Weniger reduced the number of stadia in *Eacles imperialis* and *Antheroca mylitta* from the normal six to five, by rearing them at about 25 degrees C. coupled with high humidity. By rearing the cutworm, *Agrotis ypsilon*, at 21 degrees C., 100% humidity, and at 28 degrees C., 100% humidity, in ventilated jars, the author has similarly decreased the normal number of molts by one. It is a curious fact that the cutworm, *Polia renigera*, adds one stadium to its usual number when reared under these same conditions, being affected in an opposite manner by the same stimulus.

Sexual differences in the number of stadia were first recorded by C. V. Riley in *Hemerocampa leucostigma*, the males always molting four times, the females either four or five. Payne has recorded the same phenomenon in

a few other members of this family (Liparidae). This peculiar condition has been observed by the author in but one noctuid species, *Caenurgia erechtea*. Its significance will be discussed later.

Besides these environmental and sexual variations in the number of stadia, there are very probably hereditary tendencies toward individual differences in this respect. Davis records one individual of *Cirphis unipuncta* passing seven stadia instead of the usual six. Since this exceptional individual was reared under the same conditions as hundreds of others, it seems evident that heredity and not environment must account for this exceptional instance, the possible significance of which will be considered later. Similarly, one larva of *Agrotis ypsilon*, reared with fifty-two others, molted but six times instead of seven, according to our records.

In 1890 Dyar called attention to the fact that the widths of the successive heads of any lepidopterous larva in all its stages bore a certain definite relation to each other. His presentation of this point may be summarized as follows: the quotient obtained by dividing the width of the head of any instar by that of the previous one is a constant, which is characteristic for the species. This principle has been termed Dyar's Law. Its utilitarian value is obvious, enabling one to determine what instar he is dealing with when a specimen or a published measurement of any other known instar is available. A fair indication as to the number of stadia may also be obtained if the size of the first and of the last instar is known.

An inspection of a large number of species will reveal the condition in this regard within the Noctuidae. Although the measurements represent averages derived from the number of individuals indicated, in many cases a much larger number has been examined to insure the determination of a fair average, as well as to find the extremes of variation. The material studied was either preserved when collected or grown under approximately natural conditions. Individual variation in size is not as great as might perhaps be expected, usually rendering the identification of instars a simple matter. The figures expressing the percentage of variation are obtained by dividing the maximum variation found, by the average, multiplying by 100, (to express as percentage) and dividing by 2, so that the deviation from the mean in either direction, not in total, is represented. The later instars naturally present the greatest variation, having been longer subject to external influences. Where the measurements are based on individuals of different broods the variation is usually larger than otherwise, since the larvae of certain generations often grow larger than those of others in an ordinary season. All measurements have been made with an ocular micrometer.

The inconstancy of Dyar's supposed constant, which we will refer to as the index of growth, is striking, varying in *Agrotis ypsilon*, for instance, from 1.28 to 1.84. The average for any particular species ranges from 1.44

to 1.61. The increase from first to second stadia is usually greater, from penultimate to last more often less than for other molts, this latter condition being explainable by the fact that the more rapid development of adult structures in the later instars leaves proportionately less energy available for growth. The other noticeable differences in indices of growth within a species present no uniformity. In one species, for instance, the index from second to third stadia is greater than from third to fourth, in another the reverse may be true, or in a third species these indices may be equal. The question must arise, then, as to whether the relation between these different indices within a species be definite to any extent.

An examination of the successive exuviae of isolated individuals, shows us that the variations in the index of growth for any species are of no uniformity, with the exception of the tendency toward largeness of the first and smallness of the last. All other variations are to be accounted for, then, by environment, all indices but the first and last probably tending to be equal under uniform external conditions. Any influences affecting the rate of activity of the moulting mechanism differently from that of the general metabolism must necessarily either increase or decrease the index of growth. Thus, if growth be impeded without interfering proportionately with hypodermal activity, or at least with the molting mechanism, a small index will result. Wodsedalek, by starving larvae of Trogoderma (Dermestidae), obtained many exuviae, some of the last of which were actually smaller than the earlier ones. In like manner factors favoring growth more than molting necessitate a large index.

The effect of external factors on the index is characteristic. Starvation and parasitism, of course, greatly reduce growth, but do not retard the molting processes proportionately, since the number of stadia is not affected, larvae continuing to molt when very little growth is undergone. Favorable climatic factors, on the other hand, increase the index. The unusually large increase from second to third stadia in *Agrotis ypsilon* is to be explained by the fact that the individuals upon which the given figures are based were reared simultaneously under like natural conditions, which were evidently optimum for growth, or nearly so, while these individuals were passing the second stage.

We have demonstrated the fact that some species increase in size from first to last stages considerably more than others, the total amount of growth being characteristic for the species, although variable according to external factors. It may vary widely in closely related species as in *Lycophotia margaritosa* and *infecta*. Although molting has been generally considered to be primarily a phenomenon necessitated by growth, some entomologists have been inclined to question this point, tending rather to emphasize its excretory significance. It is to be noted, however, that the seven-staged species grow more than the six-staged. This obvious

correlation between the total growth index, obtained by dividing the width of the head of the last instar by that of the first, and the number of molts lends weight to the former more general view. In Caenurgia, moreover, where there is a sexual difference in the number of stadia the females, which often molt once more than the males, average larger in size. The number of individuals of this species used in Table II is too small to justify our drawing conclusions from the fact that the growth index of the males exceeds that of the females. The fact that *Cirphis unipuncta*, which presents the greatest total growth index of the six-staged species, has been known to pass seven stadia in one instance, is of especial interest in this connection.

It follows mechanically that species with a large total increase, in other words, those with a first instar whose head is proportionately small for that of the last instar, produce eggs relatively small for their adults, the small first instar being correlated with a small egg, and the large last instar producing naturally a large moth. The egg measurements in Table I have been made from alcoholic specimens and are, therefore, somewhat larger than certain corresponding published measurements based on fresh eggs. The figures given represent the diameter of the largest circumference, the periphery of the typical noctuid egg being circular. In those species whose eggs have one diameter slightly greater than the one at right angles to it, an average has been given. Altho the correlation between egg-diameter and the width of the head of the first instar is clearly demonstrated in Table I, the ratio between these two measurements varies considerably according to the species. *Ceramica picta* presents an extreme condition where the egg is small relative to the larval head, the ratio being 1.65: In the catocalas, on the other hand, we find the width of the egg proportionately large for that of the larval head, the ratio reaching 2.62 in *C. illia*. This condition may possibly bear a direct relation to the habit of hibernation in the egg, which is general in this genus.

The shape, as well as the general internal structure of the abdomen of all noctuid moths is very nearly uniform, approximately the same proportional amount of space being used for egg-carrying in all species. It follows, therefore, that a moth producing eggs proportionately small for its size must bear a larger number than one whose eggs are large relative to the size of the adult. We should remember when considering this point that the moths of this family have but a short period for oviposition, usually laying all their eggs in a few successive nights, which permits of no egg-development during the life of the adult, such as occurs in the queen bee.

The data for the fecundity is based upon the number of fully developed eggs in the abdomens of reared moths and represents potential fecundity. Since the number of eggs actually laid in breeding cages is determined by external stimuli, all eggs in the abdomen being oviposited only under opti-

mum conditions, which for many species are difficult to obtain artificially, the published records of the number of eggs laid by various species are unreliable as indices to the potential fecundity. The undeveloped eggs, which are never laid, occupy a quite uniformly small space in the abdomen. Accurate data on fecundity can be obtained only with difficulty, since counts must be made of the eggs contained in the abdomens of moths emerging in captivity only. Moreover, a large number of individuals should be examined, because of the great individual variation in this respect. In spite of the regrettable insufficiency of data, the column headed potential fecundity presents significant indications.

A consideration of the mechanical relations already discussed enables us to understand the significance of the correlation between high fecundity and large total growth. Although a general relation between these conditions is clearly indicated, we note that certain irregularities occur. *Feltia subgothica* and *Ceramica picta* lay an exceptionally large number of eggs relative to the amount of their larval growth. An examination of the ratios between the diameter of the egg and the width of the head of the first instar in these two species reveals the fact that both bear eggs proportionately small for the size of their first instars. This condition enables the moths to lay a large number of eggs relative to the amount of larval growth for the species, accounting for the irregularity in the correlation. The relation between fecundity and growth is not direct, since the former increases more rapidly than the latter, as is evident when we read from top to bottom in these columns, a relatively slight increase in growth corresponding to a large increase in fecundity. It is highly probable that the factors determining fecundity are many. Of these factors the amount of growth is an important one in this family.

It should be noted that *Cirphis unipuncta*, with the largest total growth index of the six-staged species, having seven stadia rarely, attains the highest fecundity of those with six stadia. This destructive species has three broods in Illinois. The larvae developing in June grow markedly larger than those of the following brood, which pass the larval period in midsummer, the individuals of the fall-brood being nearly as large as those of the spring-generation. This relation probably holds only for the latitude and climate of Illinois in a usual season. Since the eggs of all generations are of the same size, the total growth is different for each brood under normal weather conditions. Altho our data as to the fecundity of the moths of different broods is inadequate, it seems quite evident that those developing from the large September larvae must have relatively high fecundity. This is suggested as a factor contributing to the fact that the spring-larvae, offspring of moths from the September larvae, almost always constitute the brood which attains such great numbers in Illinois, accompanied by the well known army-worm devastation. Altho the larvae

of this brood also attain a large size, they become greatly reduced in numbers by wilt disease and parasites, so that the midsummer -brood is usually not large. The small individuals of the midsummer-generation yield moths of low fecundity, accounting for the usual inconspicuousness of the third brood, altho infrequent outbreaks have been observed in September. It seems probable that this principle may prove to be an important one to be considered in the prediction of these outbreaks.

The fact that fecundity is hereditary in animals has been well established. Geneticists have found that the tendency to bring forth twins and triplets is hereditary in mammals. By artificial selection, Pearl and Surface have greatly increased the egg-laying propensities of a certain strain of Plymouth Rock fowls. It has been well established that fecundity in Drosophila is an hereditary trait. Individual variation in fecundity is considerable within the Noctuidae. Since those strains, in a species of this family, with a tendency to lay many eggs must transmit this trait to many more individuals than would those inclined toward low fecundity, it seems evident that in general species must increase fecundity in the course of evolution up to a point where it is checked by some sort of barrier, mechanical or physiological. The only possibility for a non-prolific strain to untimately persist would involve necessarily its accompaniment by inheritable, advantageous properties not possessed by prolific strains, such advantages offsetting their low fecundity. We have no evidence indicating that this latter, seemingly unlikely possibility has taken place within the Lepidoptera.

In the light of the correlations demonstrated, it seems evident that the amount of growth, or the number of molts, would act as a barrier to an increase in fecundity, furnishing mechanical limits, which would prevent further expression of this tendency. An hereditary increase in the number of molts, such as the one cited with regard to a single individual of *Cirphis unipuncta*, would allow the individuals possessing this trait to attain a larger size and consequently a higher fecundity. This would, therefore, be transmitted to a larger number of offspring than would the tendency toward a lesser number of molts. The persistent variation, then, would be the one with the largest number of stadia.

On the basis of this theory, the largest number of larval stages is the most specialized condition in this family. This conclusion is supported by all the other evidence available. As shown by Dyar, the great majority of lepidopterous larvae undergo ecdysis four times, five times frequently, and three, six, seven, eight, nine or ten times rarely. According to our data the molting five times appears to be the general condition throughout the Noctuidae, four molts occurring only in the two species of Phytometra, and in the male of *Caenurgia erechtea*, and six being found in but three species. We should be justified apparently in regarding the passing of

seven stadia as a specialized condition, merely on account of its exceptional occurrence.

Since the two species of *Phytometra*, *brassicae* and *biloba*, which have been reared through all larval stadia by the author, present but five stadia and *contexta*, according to Thaxter, passes six, it would seem that this biological character is not a fundamental one. The persistence of the generalized condition of molting but four times in this structurally specialized group is parallelled by the situation found in Hepialus, whose moth is very generalized structurally, but whose larva has developed the specialized habit of root-boring.

In *Caenurgia erechtea* the number of stadia presents an interesting secondary sexual character, the larva undergoing ecdysis but four times in the male and four or five in the female. The males of this species offer the only instance known to us outside of the Phytometrinae where a noctuid larva molts but four times. Parallel instances have been found by C. V. Riley in *Hemerocampa leucostigma* and by Payne in other liparid larvae, in which the male passes five stadia and the female either five or six. This phenomenon is most probably to be explained by the fact that the female larvae generally attain a larger size than the male. The fact that the female varies in the number of molts indicates further that the larger number of stadia represents the more specialized condition.

The species passing seven stadia, *Agrotis ypsilon*, *Lycophotia margaritosa* and *Nephelodes emmedonia*, do not constitute a phylogenetic unit, but have developed an extra molt independently, since each is more closely related to different six-staged groups than they are to each other. *Lycophotia infecta* undergoes ecdysis but five times. Specific differences in this respect in the genus Phytometra have already been mentioned.

POSTEMBRYONIC CHANGES

A study of the postembryology of noctuid larvae, as well as a consideration of the ontogeny of animals in general, convinces us that the structural changes exhibited in ontogeny are not all an expression of the same biological factor, but are of a number of distinctly different kinds. The structural changes appearing in the postenbryonic development of caterpillars may be conveniently classified as follows:- (1) Recapitulative; (2) Non-recapitulative; (a) Adaptive to unequal function; (b) Necessitated by the mechanics of growth; (3) Compound; (a) Recapitulative-adaptive; (b) Recapitulative-mechanical; (c) Adaptive-mechanical.

The Law of Recapitulation is of quite general but by no means of universal application, ontogenetic sequences which do not conform to the law being many and well known. The fact that a mammal at birth has a head large relative to the size of its body does not lead us to regard the ancestor

of this animal as the possessor of a proportionately large head. Nor does our knowledge of the postembryology of the house-fly convince us that it descended from an apodous insect with vestigial biting mouth-parts. We do not look to recapitulation to account for such conditions. Such postembryonic changes may be described as non-recapitulative as opposed to those of recapitulative significance, which apparently conform to the law. This point can be determined with regard to a structure undergoing change in ontogeny with a certainty proportional directly to our knowledge of the phylogeny of the structure in question. Thus, if the changes undergone by any structure in the course of its development recapitulate its race-history, we regard that structure as of recapitulative significance, but if its phylogeny be doubtful, our decision on this point must be proportionately tentative. The successive instars of species of Leucaspis figured by Lindinger reveal beyond any reasonable doubt the recapitulative significance of the pygidial structure in these coccids, the postembryology recapitulating minutely their phylogeny, which has been well established by the extensive morphological studies of MacGillivray. The recapitulative significance of wing-venation in pupal postembryology has already been mentioned. Of many parallel instances the case of Mantispa is perhaps the most familiar, the larva of this insect passing through transitional stages from a thysanuriform to an eruciform type, repeating the generally accepted phylogeny of the latter form of larva. The taxonomic advantages gained by the establishment of the recapitulative significance of a structural change in postembryology will be demonstrated later.

Many structures are adapted to the mode of life of a particular stage or to a habit associated with a single point in the life-cycle. Such organs function unequally or even differently in different stages of development, frequently being used in only one stage. Lepidopterous pupae, notably of the Sesiidae, frequently bear spines or projections used for breaking the cocoon and for wriggling into the open. These belong distinctly to the pupae. A parallel instance is furnished by the wings of insects, which function only in adults and appear in earlier stages merely as developing adult structures. Similarly caterpillars often spin silk in certain stadia and not in others, and noctuid larvae frequently do not employ the first one or two pairs of larvapods in the first stadium. This unequal function of a structure in different stages is generally correlated with structural differences, hence a non-recapitulative factor is introduced. Postembryonic changes which are the expression of this factor will be referred to as *adaptive to unequal function*. It is evident that the two factors, recapitulation and adaptation to unequal function may act in the same or in opposite directions with reference to a particular postembryonic change. In the former event it is impossible to ascertain to what extent each of these forces has operated in the production of the change, which is consequently most

reasonably regarded as the expression of the two factors combined and is referred to as recapitulative–adaptive. When these two forces conflict, the effect of the recapitulative one is completely obscured, as will be demonstrated later, the factor of adaptation to unequal function being dominant.

Since certain animal structures do not grow as rapidly as others, they are generally relatively larger in earlier developmental stages than in later. The familiar instance already cited of the newly born mammal, with its proportionately large head, is parallelled generally by insects, the heads of the first instar being markedly large relative to the body. The ocellariae and crochets of lepidopterous larvae are strikingly large in the first instar, growing slowly in comparison with the surrounding structures. These phenomena are obviously not an expression of recapitulation, but are most probably to be explained by the relative rates of cell proliferation in different kinds of tissue. This factor, like unequal function, may undoubtedly operate either with or against the recapitulative force. When the effect of the latter is obscured by that of the mechanics of growth, the resulting change is classified as *mechanical*, whereas when these two forces exert themselves in the same direction the change produced would be termed *recapitulative-mechanical*, although no clearly defined instance of this situation has been found.

The compound types involving recapitulation have been already defined. One instance noted is obviously the result of a combination of unequal function and mechanics of growth. This change is classified as *adaptive-mechanical*.

Of the possible combinations of these factors all have been actually indentified as responsible for certain postembryonic changes in noctuid larvae, except two, *recapitulative-mechanical* and *recapitulative-adaptive-mechanical*. The first of these very probably finds expression in the migration of certain head-setae to be discussed later. The second type of change possibly occurs also in these larvae.

It should be noted that, unlike the other two factors, recapitulation is to be regarded as a general law, which fails to express itself only when obstructed by other forces, which are dominant over it.

Many postembryonic changes in structure are inexplainable in the dim light of our knowledge of the factors involved. Our lack of adequate knowledge of phylogeny is probably largely responsible for this situation, since many changes such as those of the head-capsule of muscid larvae figured by Nielsen, may prove to be of recapitulative significance, when sufficient morphological work is done to establish the race-history of such structures. An investigation, moreover, of the functions in different stages of organs undergoing postembryonic changes will most probably reveal many instances of adaptation to unequal function, while the determination of the importance of the factor of the mechanics of growth awaits the re-

searches of the histologist. Hence morphological, biological and histological investigation may be expected to explain for the most part these numerous problematical changes, such as those in the shape of the body-setae and of the antennae of caterpillars, in the number of facets in the eye of the nymphs of dragon-flies, in the heads of muscid larvae, in the structures of the caudal end of the body of tipulid larvae, in the number of tarsal segments in the Heteroptera, and many others. Such investigations will probably reveal a number of types not listed in our present classification, which is necessarily very restricted, applying only to noctuid larvae.

The postembryology of the fixed parts of the noctuid larval head reveals the following changes:

(1) Appearance of the adfrontal sutures; (2) Change in the relative length of the epicranial stem; (3) Mesal extension of the postgenae; (4) Change in the shape of the labrum; (5) Reduction in the relative size of the ocellariae and sensoria; (6) Change in the position of the setae; (7) Change in the shape of the setae; (8) Change in the coloration.

ADFRONTAL SUTURES

Although the presence of the adfrontal sclerites has long been regarded as a condition diagnostic for lepidopterous larvae, the fact that this area appears only in the later stadia, at least in noctuid larvae, has apparently not been discovered. Very frequently the coloration of the early instars gives the appearance of adfrontal sclerites where no structural differentiation exists, which has most probably been conducive to the general overlooking of the true situation. In the noctuids these sutures are distinct only in the larvae of the two later stadia, very faint indications being sometimes distinguishable in exuviae or treated heads of the third from last stage. The adfrontal sclerites have been regarded as bearing a direct structural relation to the infoldings along the epicranial arms. Fracker speaks of them as the "external expression of the attachment of the anterior arms of the tentorium." An inspection of a section thru this region (Fig. 1) reveals absolutely no connection between the adfrontal suture and the epicranial parademe, to which the pretentorium is attached. This suture appears externally as a narrow light-colored line constant in general position throughout the family but varying much in its irregular curving, even within a species. In sections it is not distinguishable from the general cuticle, except by its lighter pigmentation. Since the older ideas of its significance are obviously incorrect, our present problem is to account for its existence.

The usual place of splitting in the head-capsule at molting and at pupation is along the epicranial stem and arms in all but the more specialized forms such as dipterous or coccinellid larvae or coccid nymphs. We regard this, therefore, as the generalized condition in insects. As was stated in

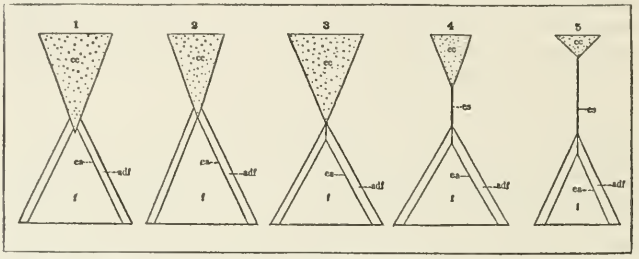
our consideration of the morphology of the tentorium, the great reduction of this originally supporting structure has been accompanied by the development of a number of deep infoldings, one of which occurs along the epicranial suture. As might be expected, the marked specialization in this region is accompanied by a specialized condition in molting, the entire head-capsule being shed intact. So far as we know the larvae of no other order molt without breaking the exuvia of the head, altho some nymphs do so. It seems probable that the deep infolding along the epicranial suture has rendered the usual splitting impossible. The great change in form undergone at pupation, however, makes a break in the last head-capsule mechanically necessary. This occurs along the epicranial stem and adfrontal sutures. So far as we have been able to determine they have no other function. These structures are to be regarded, then, as a modification for pupation due indirectly to the greatly reduced condition of the tentorium and to the deep parademe along the epicranial suture, which has taken over the supporting function of the tentorium.

The well developed condition of these sclerites in the next to the last instar, where they do not function, is paralleled by the general occurrence of adaptive structures in stages earlier than the one in which they are used. Altho the adfrontal sutures appear in larval development as they presumably did in phylogeny, beginning as a very faint line which becomes prominent later, the fact that they function only in the last instar indicates that the factor of unequal function also plays an important part in their development. If recapitulation alone were operating on this postembryonic change, we should, moreover, expect these sutures to appear in the first instar, as shown by the following facts. Their universal occurrence throughout the order indicates very strongly that they were present in the ancestral lepidopterous larva. Since the first instar of the noctuid larva is typically noctuid, it presumably represents with reference to recapitulation a period in phylogeny later than the one in which the Noctuidae appeared, certainly much later than the period in which the adfrontal sclerites originated. Hence on the basis of recapitulation alone the first instar would exhibit well developed adfrontal sutures. Their failure to appear until late in larval development is evidently due to the fact that they function only in the fully grown larva. This postembryonic change is evidently the expression of the two factors recapitulation and unequal function and is to be classified as recapitulative-adaptive.

EPICRANIAL STEM

As has already been shown in our consideration of the morphology of the head, the relative length of the epicranial stem varies widely in the larvae of this family, (Figs. 2, 15, 16, 17) furnishing a character second only to the number of larvapods in conspicuousness. The proportional length of

this suture is most conveniently expressed in terms of its ratio to the length of the front. The quotient obtained by dividing the length of this sclerite by that of the epicranial stem will be referred to as the epicranial index and expressed by F/Ep. The great majority of lepidopterous larvae have a fairly long epicranial stem, Types 4 and 5 predominating. Type 5, with the epicranial stem longer than the front, occurs more frequently than Type 4, with the front exceeding the stem in length, in the Noctuidae and their allies, as well as in the Sphingidae and Rhopalocera. The average epicranial index normally found in the Noctuidae is about 0.7, the stem being somewhat longer than the front. Within the great superfamily Noctuoidea, the markedly short epicranial stem occurs only in certain genera of the Noctuidae. This condition is very frequently seen, nevertheless, since



Hypothetical figures showing the relation of the front and epicranial stem. *adf*, adfrontal sclerite; *cc*, cervacoria; *ea*, epicranial arm; *es*, epicranial stem; *f*, front.

many of our commonest and most economically important noctuid larvae present this type of head. The infrequent occurrence of the reduced epicranial stem in the Noctuidae and allied families indicates that this is a specialized condition, at least in this group.

Moreover, wherever found in lepidopterous larvae, the short epicranial stem is associated with a specialized feeding-habit, that is, a habit other than the usual leaf-eating one, which we may reasonably attribute to the ancestral lepidopterous larvae, on the basis of its general occurrence in existing forms. Similarly, the parasitic life of certain of the family Orygsidae is to be considered as a specialized one, since the larvae of the horntails are typically borers. Leaf-mining larvae whether coleopterous, dipterous, or lepidopterous furnish an instance of specialized habit. The root-boring habit of the larvae of Hepialus is to be regarded as a biological specialization, altho their adults are structurally generalized. The larva of the noctuid, *Epizeuxis lubricalis*, feeds upon dry dead-wood, that of *Scolecocampa liburna* on moist dead-wood. Various cut-worms are subterranean to a greater or less extent. Each of these modes of feeding

represents a departure from the leaf-eating habit and free-living existence, which were most probably characteristic of the ancestral lepidopterous larva.

There is a correlation between the short epicranial stem and specialized feeding-habit. It will be seen that Types 1 and 2 occur only in leaf-miners, Type 3 being also confined to larvae of this habit except in the seed-eating or stem-boring Prodoxidae, in the wax-eating bee-moth larvae, and in the leaf-rolling Tortricidae. Similarly in the Noctuidae the reduced epicranial stem is always associated with a specialized habit, the subterranean mode of life. The more pronounced this habit the shorter is this suture.

It has been necessary in order to establish this correlation to find criteria by which we may compare larvae of various species with reference to their subterranean proclivites. Cut-worms have generally been described in economic literature as larvae which hide beneath the ground by day, eating at or beneath the surface during the night. Our experiments have shown, however, that there is considerable diversity of feeding-habit, even within this biological group. Certain so-called cut-worms never enter the soil, others do so only under extreme stress, and some, on the other hand, never come above ground except for ecdysis. In addition to observations made on larvae reared under natural conditions, two series of experiments have been performed to determine the relative extent of the development of the subterranean habit with as many species of noctuid larvae as possible. The first of these determines which species are able to burrow into the soil and to what extent this ability has been developed in each. The second series of experiments determines the extent of the power to resist submergence in water, a resistance which subterranean animals have generally developed. The combined results derived from these two lines of investigation enable us to form a fairly accurate idea as to relative "subterraneanness" of various species. We will now consider these experiments.

DETERMINATION OF BURROWING HABIT

The determination of the relative extent of the development of the power to burrow into the soil in the larvae of various species is the object of the first series of experiments. The logical method for making manifest an ability or tendency to burrow into the ground, however slight, involves the subjection of the organism to an irritating factor to which it reacts in a markedly negative manner, at the same time excluding all means of avoiding this factor except by entering the soil. Lepidopterous larvae generally avoid direct sunlight, a large proportion of them being nocturnal in habit. This is especially true of noctuid larvae, the cut-worms being notoriously active at night. Altho precise experiments on the reactions of these insects to light are much to be desired, anyone who has worked with them extensively will have noticed, without doubt, a generally marked

negative response to light. The author knows of no other natural factor calling forth such immediate and pronounced response. These experiments have been performed, therefore, in the following manner:

An ordinary fifty watt electric light bulb was suspended above the center of a glass-jar three inches in diameter, containing soil, with the lowest point of the bulb six inches above the soil. A thermometer was suspended with its bulb touching the soil in the center of the jar. The typical black earth of Illinois was used in a finely pulverized condition and sufficiently humid to eliminate dust. It was packed down lightly on top, leaving an even surface. The temperatures ranged from 33.3 to 35.5 degrees C. which was much higher than that of the laboratory due to the heat from the light. Except in Experiment 3 all material used was reared outside under approximately natural conditions and well fed. It was not brought into the laboratory until immediately before the experiment was to be started, except in Experiment 3. To avoid interference with one another, not more than five larvae were put together in the same jar. Frequently several instars of the same species were used, altho they always reacted alike, so far as could be observed. Observations were taken every few minutes, account being kept of the time required for the larvae to become visibly stimulated, as well as of the time elapsed before each individual should become buried, wholly or partially. These experiments were performed in April and May, except where otherwise indicated in the tables, consequently the temperatures to which the larvae were subjected during the experiments were unnaturally high, probably adding to the irritation produced by the light.

It has been shown that stimulation is usually immediate. Well fed larvae, which lie motionless when brought into the laboratory from the outside, generally exhibit pronounced irritation as soon as subjected to the light, running rapidly about the jar. The phrase "time required for submergence" expresses the time from the beginning of activity to the time when the individual is entirely or partially buried. In several instances certain individuals ceased activity as soon as the head and thorax were beneath the surface. This feature seems to be an individual rather than a specific trait. While the larvae of some species commence burrowing within two or three minutes after they become stimulated, entering the soil perpendicularly and disappearing within a few seconds after they begin to dig, others crawl for half an hour, making an occasional abortive attempt to thrust their heads beneath the earth, finally very gradually burying themselves by entering the soil at a small angle with the surface. Other species make no attempt to burrow, continuing to crawl actively about for two hours, at the end of which time the experiments were usually ended. We find represented in these species evidently several stages in the development of the subterranean habit, some entering the soil very readily, others with apparent reluctance, and some not at all.

Unavoidable differences in the physiological condition of the individuals account, most probably, for the considerable variation in the "time required for submergence" with different larvae in the same experiment. During the rest period prior to ecdysis and some six hours before it, larvae make no attempt to burrow when subjected to the test, no matter how pronounced this habit may be in the species. Three individuals of *Polia renigera* which reacted differently from the rest, failing to enter the soil, were isolated and found to be parasitized by chalcids when they died several days later. One larva of *Agrotis c-nigrum*, presenting a similar non-conformity to specific habit, died of the fungus, *Botrytis rileyi*, some time afterward. This individual revealed a marked negative geotropism, crawling up on the sides of the jar and onto the thermometer, a reaction exhibited by no other larva investigated. It is interesting to note in this connection that grasshoppers diseased by *Empusa gryllidae* and army-worms or cut-worms affected by wilt present the same response, crawling always to the top of some plant to die. Underfed larvae require a much longer time to bury themselves than do well-fed ones of the same species, the hunger stimulus seeming to partially overcome the negative response to light. Experiment 3 illustrates this point very clearly, the material having been kept without food for twenty-four hours in the warm laboratory at a temperature at which the metabolism is high. Since the larvae were very hungry, they resisted the tendency to burrow for a much longer time than in the other experiments, where they were well-fed. For this reason the averages given in this table do not include Experiment 3. The difference in the time of day when these experiments were performed bears a direct relation to the hunger, since the larvae feed principally at night. In Experiment 1, performed at 9 P.M., the slower response may be due to the fact that feeding was interrupted. The difference in weather conditions prior to the performance of Experiments 1, 2, and 4, undoubtedly has contributed further to the lack of physiological uniformity in the material used, introducing an additional source of error.

Altho accurate data as to the relative facility with which various species enter the soil can be obtained only by a long series of experiments carried on under carefully controlled conditions, employing a much larger number of individuals than have been available for use in our investigation, the data presented afford, nevertheless, some significant indications. Since species such as the arboreal *Homoptera lunata* or the cabbage looper, *Phytometra brassicae*, which we know to be not subterranean, are not induced to enter the soil under the conditions of the experiments and since notoriously subterranean species readily manifest their ability to burrow when stimulated by light, we are justified in applying this test in order to determine whether larvae have subterranean tendencies in species with which this point is doubtful. It has been determined thus that the bronzed cut-worm,

Nephelodes emmedonia, and the cut-worms of the genus Cirphis (the army-worm genus) are not subterranean. Furthermore, in the subterranean species the relative facility with which the larvae enter the soil, as indicated by the "time required for submergence," as well as by various peculiarities already discussed associated with burrowing, serves as an indication of the extent of the development of the subterranean mode of life in these species. It may be noted, for example, that *Sidemia devastatrix* presents an extreme case of development of the under-ground mode of life in noctuid larvae. The larva of this species rarely comes above the surface except to molt. Unlike other cutworms it has lost its body pigment and has been aptly described as "half way between a cut-worm and a white grub." Owing to the insufficiency of material and to the sources of error previously mentioned, it would seem unwise, however, to attach undue significance to the relative lengths of time required for burying given in this table.

RESISTANCE TO SUBMERGENCE

The object of the second series of experiments is to determine the relative resistance to submergence in water in various species of noctuid larvae. Immediately after an unusually heavy thunder-shower, several arboreal noctuid larvae were found dead, clinging to the trunks of trees in crevices in the bark, where water had been running during the hardest part of the rain, which had lasted about twenty minutes. Since lightning had not struck in the vicinity, it seemed evident that these larvae were drowned by the water running down the tree-trunks. They bore the characteristic marks, to be described later, of drowned larvae. A few days afterward a cut-worm, *Feltia subgothica*, accidentally left in water for two days in the laboratory, recovered after a number of hours and resumed feeding. This striking difference in the ability to resist submergence in water between the arboreal caterpillars and the subterranean Feltia suggested the use of the length of time during which larvae could resist such submergence as an index as to the extent of the development of their subterranean habit. During early spring land infested with cut-worms, many of which hibernate as partly grown larvae, is often saturated with water for days at a time, without seemingly affecting their numbers. We should naturally expect such insects to be able to withstand these conditions successfully and to have developed, in common with subterranean animals generally, a resistance to submergence. Non-subterranean larvae of the ground- and field-strata might be expected to possess this power to a lesser extent, and arboreal species would presumably lack it almost entirely, since the nature of their habitat usually renders it unnecessary for them to withstand extensive drenching. Caterpillars which hibernate in the soil must be subjected to water from the melting snows as well as to the spring rains and consequently might reasonably be expected to present the most extensive resistance to submergence of any lepidopterous larvae.

This subject has been investigated experimentally in order to obtain so far as possible a means of expressing mathematically the relative "subterraneanness" of various species of noctuid larvae. The material used in these experiments was reared under approximately natural conditions. Before being submerged in water the larvae were washed to remove all soil and particles of foreign matter such as might carry minute air bubbles beaneath the surface. Immediately after washing, each larva was put in 150 cc. of distilled water five cm. deep contained in a small glass jar. When the larvae were small, two or three were usually put together in the same jar. In order to keep conditions as constant as possible throughout this series of experiments, the jars were kept in a constant temperature chamber at about 17 degrees C., there being occasionally a deviation of one or two degrees in either direction for a few hours at a time. They were exposed to natural light but not to direct sunlight. At the end of the period of submergence the larvae were dried on filter paper, then placed on a blotter six inches below a fifty watt Mazda electric light. Subjected to the stimulation of this irritating factor, manifestations of life could be most readily brought forth. While in this situation, the time required for the individuals to regain various degrees of activity was recorded. They were kept under the light for lengths of time varying from fifteen minutes to three hours or more, depending upon the readiness with which activity was regained. When stimulated as much as possible by this means, the individuals were isolated, each being placed under approximately natural conditions with food, in order that observations on the later effects of submergence might be made for several days.

The first few seconds of submergence are always spent in violent movements of the entire body, after which the larva suddenly becomes motionless, remaining so until removed from the water. Individuals undergoing ecdysis float, necessitating their being weighted down by a small piece of metal tied to the anal uropods by a fine thread. It seems probable that there may be a layer of air between the old and new cuticle, which would account for the low specific gravity of larvae in this condition. When not molting, they always sink immediately. After being removed from the water, dried, and placed under the light, the first signs of life are usually represented by the beating of the heart, which can be observed according to the transparency of the integument. Slight movements of the antennae and thoracic legs are next to be seen, followed by a feeble curling of the thorax caused by contractions of the longitudinal muscles, often accompanied by an extension and retraction of the crochets. As various kinds of motion of the trunk and appendages become more marked, water is expelled in quantity from the mouth and anus. When in this stage of recovery, larvae placed with the ventral surface uppermost gradually turn over. Sometime later they will crawl a little when mechanically stimu-

lated, still expelling water. Often after a few hours they appear normally active, altho seldom feeding until several hours after apparent recovery. The evidences of the regaining of activity take place almost invariably in the above order.

The stage of activity reached with individuals which fail to recover varies according to the resistance of the species and to the length of time submerged. When kept under water for a time much longer than that required for drowning, sometimes no movement can be produced by stimulation. More often, however, the earlier stages of activity are passed through, followed by a decline evidenced by a repetition of the same stages in reverse order. Frequently larvae which have apparently thoroly recovered, crawling actively about, refuse to eat and die within two or three days. This indicates that the length of time for which they were submerged is very close to the minimum time required for drowning for the species in question.

The extent of activity developed before the decline sets in offers a valuable guide to the determination of the minimum time required for drowning, which is the object sought in these experiments, since this factor enables us to express in numbers the resistance to submergence of various species. From the data collected it has been possible in most cases to determine within rather narrow limits the average minimum time required for drowning. When one-half or one-third of the individuals of an experiment die and the rest survive, the time for which they were submerged is taken as representing approximately the resistance to submergence for the species.

Altho different instars of the same species present no uniform difference in resistance, we find some individual variation in this respect, which is most probably to be accounted for by unavoidable physiological differences in the material. Such factors as the time expired since molting, the amount of food in the alimentary canal, and the weather conditions under which the material was reared undoubtedly influence the resistance to submergence to a greater or less extent. The first of these, which will be discussed later, is probably the most important. It is to be regretted that data regarding the resistance of larvae of different broods have not been obtained, since such data would be of considerable interest with respect to those species having several broods a year and hibernating as partly grown larvae. Our experiments with such species have been performed solely with larvae of the hibernating brood after hibernation had been passed. Very probably those of the summer broods are less resistant. If this be true, it would be of great interest to determine whether the difference in resistance in different broods is innate or induced by climatic factors.

The specific variation in resistance to submergence is extreme, ranging from 25 minutes to 48 hours. The exact nature of the adaptations, mor-

phological or physiological, which permit of such striking differences in this respect, is problematical. We find no external structures which throw light on this question. The spiracles offer no variations which seem to bear on this point. Internal structures or histology, a study of which the scope of this work does not permit, may be found to bear relation to the development of the power to withstand submergence. It seems probable that differences in the efficiency of the mechanism for closing the tracheae just entad of the spiracles may be found.

There are indications that death from drowning in these larvae is caused by two factors, oxygen starvation and mechanical injury due to the filling of the alimentary canal with water. The drowned larvae have always exhibited a black girdle around the body, varying in extent from one segment to five or six, so that in the latter case it extends for half the length of the larva. Those which almost recover from submergence show but a slight ring around the metathorax or first one or two adbominal segments, while individuals which die before their removal from the water often turn black from the head to about the sixth abdominal segment. Larvae killed by pinching have exactly the same appearance. This appears to indicate mechanical injury caused by distending the alimentary canal with water. The expulsion of water from both mouth and anus during recovery has already been mentioned. It is a significant fact that larvae in the prepupal condition and those undergoing ecdysis are much more resistant than others. Of these the prepupae swallow water and the moulting larvae do not, owing to the fact that the mouth-parts cannot function during ecdysis; yet the former show at least as great a resistance as the latter. Larvae passing through these two stages are physiologically similar in the following respects: they are quiescent; they are not digesting food, having expelled the contents of the alimentary canal; and they are preparing to shed their cuticle. We have reason to suppose that the oxygen requirement for both prepupae and molting is relatively low, due to the reduction of motion and to the lack of digestion of food. In the light of this probability the great resistance to submergence of larvae in both of these stages becomes understood. Death by drowning seems to be effected, then, both by lack of oxygen and by mechanical injury due to gorging the digestive tube with water. How subterranean larvae are equipped to withstand either or both of these factors, we do not know.

The resistance to submergence in different species, as determined experimentally, varies according to the extent to which the larvae are subjected to submergence or to drenching in their natural habitats. This resistance is not only correlated with the proximity of the habitat to the ground during the active life of the larva, but also with the stage in which the hibernation is passed, since larvae passing the winter in the soil must withstand considerable submergence without regard to their habitat while

in an active condition. In order to present more clearly the relations shown in the data collected, it has been divided into two sections, the first of which includes only those species hibernating as larvae on or beneath the ground, the second section embracing those not passing the winter in this stage. If we compare two equally subterranean species, one of which hibernates in the soil as a larvae, the other as a pupa, we note that the former is very much more resistant to water. *Feltia subgothica* and *Agrotis ypsilon* or *Nephelodes emmedonia* and *Phytometra brassicae* afford examples of this point. It is evident, then, that we should confine our comparisons of the resistance to submergence of species, with reference to their habitats, to those which fall in the same section. By so doing the factor of the stage of hibernation is eliminated.

It has been found that the subterranean species present the greatest resistance. *Epizeuxis lubricalis*, because of its exceptional mode of life, cannot properly be compared to other species in this section. Altho never entering the soil, it remains in wet weather in or beneath water-soaked pieces of decaying wood on the ground, dead-wood furnishing the food for this biologically specialized species. Consequently, it presents a high resistance, altho non-subterranean. The relative development of the power to resist water in species of the subterranean-, field-, and tree-strata is indicated in Section 2, in spite of the insufficiency of the data. Most resistant is the fairly subterranean *Lycophotia margaritosa*, next the non-subterranean cabbage looper, *Phytometra brassicae*, of the field-stratum, and least so the arboreal forest-species, *Homoptera lunata*.

EPICRANIAL INDEX AND SUBTERRANEAN HABIT

This investigation of the resistance to submergence in water leads us to conclude that this factor is an index to the extent of the development of the subterranean mode of life, altho hibernating larvae cannot be directly compared in this respect with those not passing the winter in this stage. We have now established two criteria for determining the relative "subterraneanness" of species, namely, the readiness with which the larvae enter the soil and their resistance to water. The latter, since it is capable of numerical expression much more accurately than the former, is far more significant as a guide to the extent of the development of this habit.

It has been stated previously that the epicranial index is correlated with the subterranean habit, those species presenting the most marked underground mode of life having the shortest epicranial stem. Having necessarily disgressed from our principal line of thought, in order to establish the relative "subterraneanness" of various species, we are now prepared to continue our consideration of this suture. We have already shown that the short epicranial stem or large epicranial index isan exceptional condition in lepidopterous larvae, associated with a specialized feed-

ing habit. The data confirms not only that this condition in the Noctuidae is confined to subterranean larvae, but that the extent of the development of this habit is correlated very definitely with the relative length of the epicranial stem. We have ample reason, therefore, for stating that the short epicranial stem is a specialized condition in noctuid larvae, associated with a specialized mode of life, the subterranean one.

Our understanding of the mechanics of this correlation is by no means complete. Subterranean larvae are characterized in general by an extensive chitinization of the pronotum, beneath which the caudal part of the head is retracted most of the time. The mouth-parts tend to become directed cephalad instead of ventrad in such larvae. A parallel, but more extreme condition is exhibited by the lepidopterous leaf-miners, where we find the greatest reduction of the epicranial stem correlated with mouth-parts directed cephalad, the caudal portion of the head remaining beneath the chitinized pronotum. It seems evident that mandibles in this position are better adapted for burrowing than those directed ventrad, and that this change in the position of the head has induced a shortening of the epicranial suture, a point which has been discussed in the morphological section of this paper. When we consider the profound specialization in the heads of beetles, which has been brought about in correlation with the change in the position of the mouth-parts from a ventral to a cephalic direction, it seems quite reasonable to suppose that a less marked specialization in the position of the head, such as we find in subterranean noctuid larvae, would be accompanied by proportionately less pronounced modifications of the head-capsule.

Our knowledge of this relation between the epicranial stem and the feeding habit should be of some value to the economic entomologist. Cut-worms attacking well-cultivated crops, such as corn or tobacco, must be able to enter the soil in order to protect themselves from the heat of the sun. The larvae of those species which do not burrow must depend upon an abundance of grass or weeds, among the bases of which they can withdraw during the brighter part of the day. Noctuid larvae with a long epicranial stem, such as the bronzed cutworm, *Nephelodes emmedonia*, or the members of the genus Cirphis, to which the army-worm belongs, are unable to enter the soil and are therefore seldom found attacking well cultivated crops. When such crops are attacked by army-worms, it is during migratory outbreaks, when their reactions are abnormal. It is a significant fact that all of the fourteen species dealt with by Crumb in his key to tobacco cutworms are of the short-stemmed type. The army-worm's abstinence from tobacco is not a matter of appetite, since this author has found them to eat it as readily as grass, but it is rather because of the inability of this species to burrow into the earth and thus escape the rays of the sun. Hence an examination of the length of the epicranial stem of an

undetermined cutworm may inform the field-man whether or not it could consistently attack any well cultivated crop.

The changes in the epicranial index, length of front divided by length of epicranial stem, undergone in the postembryology of various species are presented in the tables. The percentage of variation has been computed in the same way as in Table I. The measurements were made with an ocular micrometer. It will be noted that the greatest individual variation occurs in the last instars of the most subterranean species, which present the most specialized condition of the epicranial stem. The postembryonic development of the epicranial index has been graphically expressed in Plate I. The horizontal axis has been divided into six equal parts representing stadia, this being the usual number within the family. With those species presenting five or seven stadia, the units on the horizontal axis have been respectively lengthened or shortened so that the total length of this axis remains the same for all curves. By this means curves of species having a different number of instars can be more easily compared. The interpretation of this chart presents some very significant points, which we shall consider singly. These curves may be conveniently divided into two types. The curve of the first type turns upward toward the right and shows a marked shortening of the epicranial stem in the later stadia, while that of the second type continues downward and reveals a continuous lengthening of this suture. The significance of this turning upward, presented by the first type, will be considered at this point.

It has been well established in our discussion of the phylogeny of this structure that in this family the short epicranial stem has descended from the longer more primitive one. Since the curves of those species whose last instars present a reduced condition of this suture reveal the presence of a longer one in one or more of the preceding stadia, we must conclude that the postembryology of this structure recapitulates its phylogeny. In our classification of the kinds of postembryonic changes, those involving the relative length of the epicranial stem fall, therefore, under the recapitulative type.

The curves of all species of Noctuidae examined reveal a lengthening in the stem from earlier to later stadia or to the stage in which the turning upward takes place. In the three species examined representing the families Notodontidae, Liparidae, and Psychidae, we find this same condition, altho not very marked in the first of these, indicating apparently that this suture was short in the ancestral larva of these families, and possibly in all the Lepidoptera. We have, however, no phylogenetic evidence in support of this indication, since the larvae of the most generalized families usually have specialized feeding habits, rendering it unsafe to regard a structure whose condition is correlated with the feeding habit, as we have shown that of the epicranial stem to be, as representing a generalized con-

dition in these larvae. This suture is fairly long in the root-boring larvae of the three species of Hepialus examined. In the larva of the European cossid, *Cossus cossus*, we find an unusually short epicranial stem, while *Zeuzera pyrina* shows the opposite extreme, altho both are borers in live-wood. The bag-worm, *Thyridopteryx ephemeraeformis*, offers an average condition of the epicranial index. It is probable that none of these species presents a generalized condition with respect to this structure, altho they represent generalized families. Since the turning upward toward the right of the chart, wherever it is found in these curves, evidently expresses a recapitulation of the phylogeny of this structure, it seems reasonable to conclude that the turning downward toward the left in the same curves represents also a recapitulation. The lack of change in epicranial index from first to second instars in the two species of Phytometra examined, as well as the turning upward shown by the curves of various other species, precludes all possibility of explaining this lengthening of the epicranial stem in terms of the mechanics of growth. There is no mechanical force, in other words, producing more rapid growth in the vertex than in the front. Hence, in the absence of knowledge concerning the early phylogeny of this suture, such data as we have indicate that the ancestral noctuid larva possessed a short epicranial stem, altho this condition is found in existing forms only as a secondary development associated with the subterranean mode of life.

We will consider now the interpretation of the fact that the change in direction in those curves which turn upward takes place in different stadia in different species. This interpretation involves, in the first place, an analysis of the postembryological relation which corresponding stadia in different species bear to one another. Do corresponding instars in species having the same number of stadia necessarily represent identical post-embryological stages? Various mammals at the time of their birth present somewhat different developmental stages. The kangaroo, for instance, brings forth its young in a very immature condition, corresponding to that found in the late embryonic life of the majority of mammals. It seems not unlikely that insects may offer a parallel situation, the early postem-bryonic life of some corresponding, perhaps, to the latter embryonic life of others. Within a group as closely related as the noctuids it seems very improbable that such a condition should exist to any appreciable extent, altho we cannot be sure that all noctuid larvae are equally mature at hatching. However, this may be, it is certain that the passing of cor-responding stadia requires quite different proportional lengths of time in different lepidopterous larvae, even within the same family, suggesting the possibility that the postembryological value of such stadia may differ according to the species. If we find, for example, the first stadium of one species requiring one-third of the total larval life and that of another species

but one-eighth, we naturally begin to doubt that this stadium represents the same stages of development in these species. The data presented will serve to illustrate this condition. We note that the time required to pass various stadia relative to the total larval life varies considerably in species and to some extent in individuals. The question arises as to how much of this difference is due to external factors and what proportion of it is attributable to innate tendencies. The effects of change of temperature, of starvation, and of parasitism upon individuals of *Polia renigera* are very marked, as is the influence of seasonal conditions upon different broods of *Coramica picta*, demonstrating the pronounced effect of external factors upon the length of stadia. The innate tendencies in this respect can be determined accurately for various species only by rearing their larvae under constant conditions, as has been done with *Polia renigera* and *Agrotis ypsilon*. These were reared at both 28 degrees C. and 21 degrees C. in ventilated jars at 100% relative humidity. The individual variation in the relative length of the stadia of the few individuals which were so reared we cannot satisfactorily explain. Larvae of these two species reared outside do not differ uniformly in the proportional length of their stadia from those grown under constant conditions.

The lack of data derived from rearing larvae in this manner precludes our drawing definite conclusions as to the innate relations existing between the duration of different stadia in different species. Nevertheless a comparison of species reared outside may offer us significant indications regarding this point. It will be noted that the larvae of two species of tussock-moths, *Notolopha antiqua* and *Hemerocampa leucostigma*, which were reared by Payne in Nova Scotia under natural conditions, present a relatively long first stadium. Larvae hatching from forced hibernating eggs of the latter species in Illinois and grown in a warm laboratory by the author also required an unusually long period for passing this stadium, indicating that this unusual condition is not to be explained by the effect of external conditions upon the larvae. Nor is it correlated with hibernation in the egg stage, since three species of larvae of Catocala hatching from hibernating eggs about the same time failed to show this condition, the first and second stadia requiring about an equal amount of time. In all noctuid larvae reared by the author the last stage has been markedly the longest, whereas in these two species of liparid larvae the last two stadia are nearly equal in duration. The three larvae of *Dipterygia scabriuscula*, showing the long first stadium, hatched on the same day as the fifty-one individuals of *Agrotis ypsilon* and were reared under the same conditions, yet all of the latter species required approximately the same amount of time for passing first, second, and third stages. In *Polia renigera* there seems to be a general increase in the length of the two latter stadia, while only the last stage is long in *Agrotis ypsilon* and *Lycophotia margaritosa*. These facts all indicate

the presence of innate differences in the relative length of corresponding stadia in different species, even within families.

The presence of such a difference, however, need not necessarily indicate a difference in postembryological value of the corresponding stadia of the species compared, since the longer stadia may be associated with slower development. The fact that the amount of increase in the width of the head-capsule from one stage to the next remains practically constant for the species, bearing no relation apparently to the duration of the stadia, shows that the longer stadium represents the slower growth. For example, *Dipterygia scabriuscula* requires a much longer relative time for passing the first stadium than does *Lycophotia margaritosa*, yet both species grow approximately equal amounts during this stage, the former growing more slowly than the latter. Since the first instars of these two species grow relatively the same amount, it seems quite probable that they present the same postembryological stage at the end of the first stadium, nowithstanding the specific difference in the duration of this stadium. However, this is not necessarily true, for it is easily conceivable that corresponding instars of two species might grow relatively equal amounts and yet attain different stages of development. Much investigation on the postembryology and physiology of these larvae must be completed before we shall be able to settle definitely this question as to the exact relations which the duration of the stadium and the amount of growth bear to the stage of postembryonic development.

It is highly probable, however, that corresponding stadia in closely related species represent about the same stages in postembryology. Altho the first stadium of one species may possibly correspond embryologically to the first and part of the second in another or perhaps the third instar of one may represent in development the latter part of the third and first half of the fourth in another, it seems practically impossible that the developmental differences within this family could be sufficiently profound to render the first stadium of one species equivalent postembryologically to the third of another or the fourth of one to the sixth of another. Whatever minor variations in this respect may exist in those species whose curves turn upward would certainly not be sufficiently extensive to mislead us in interpreting these curves.

From our conception of the law of recapitulation it follows as a corollary that identical stages of development in different species must represent the same period in phylogeny with reference to the recapitulation of a particular structure. This corollary may be stated thus: Any recapitulative change must recapitulate in equivalent stages of development in different conditions of species which have developed during the same phylogenetic period. It follows, of course, that postembryological stages which are not equivalent must present conditions with respect to a particular recapitula-

tive change which have developed at different times in race-history, the earlier stage in the ontogeny representing the earlier phylogenetic period. For example, when we find the epicranial stem, which we have shown to be a recapitulative structure, beginning to shorten in the second stadium of one species and not until the fifth of another, we conclude that this condition developed in the former species in a much earlier phylogenetic period than in the latter.

We cannot be reasonably certain of locating equivalent postembryological stages in different species unless they be rather closely related. In attempting to find developmental stages in a lepidopterous and a coleopterous larva, for instance, which we could be certain were identical, we should encounter, no doubt, considerable difficulty. The former might be more mature at hatching than the latter and they might pupate at somewhat different postembryonic stages. Furthermore, various structural and developmental specializations might render it practically impossible to locate exactly corresponding postembryological conditions in the larvae of these two orders. Tower has shown that beetle larvae present marked developmental diversity within themselves, the wings of certain chrysomelids being distinguishable at the time of hatching from the egg, whereas in the Curculionidae, and some other families they do not appear until the last larval stadium. By going back sufficiently far into the embryology we could undoubtedly locate equivalent stages in the most diverse orders of insects, but in the postembryology we must confine the application of this corollary to closely related species, where no marked developmental or structural diversity threatens to mislead us.

We have already concluded that corresponding stadia of those species whose curves turn upward may be regarded as representing approximately equivalent postembryonic stages. It becomes evident upon the application of the corollary just discussed that these stadia also correspond to more or less definite periods in phylogeny. Each unit on the horizontal axis of the chart represents roughly, then, a definite postembryological stage and an equally definite period of time in race-history. The relation which these units bear to one another we need not consider at this point. It will be shown later that certain biological evidence supports the application of this corollary to our intepretation of these curves.

Plate I shows conclusively that the short epicranial stem has appeared independently in different species during widely separated periods in the ancient history of this family, since the shortening of this suture begins as early as the second period in some but not until the last in others. Hence the short-stemmed species do not constitute a phylogenetic unit, a point which will be discussed in detail later.

The progressive nature of the tendency toward the shortening of the epicranial stem is very apparent in these curves which turn upward. In

but one or two instances among the noctuid larvae examined has the relative length of this suture remained unchanged after it has ceased to lengthen and never has it grown subsequently longer after once beginning to shorten, but it has continued to become progressively more reduced with the passing of time. The species which began to exhibit this reduction earliest in their race-history generally present the shortest stem in their last instars. This does not necessarily hold true in all cases, however, since some species had a much longer epicranial stem than others at the time when this suture commenced to decrease in length, so that the greatest reduction in the last instar is not always correlated with the earliest appearance of this shortening. A comparison of the curves of *Polia renigera* and *meditata* will serve to illustrate this point. Moreover, there is a marked diversity in the angle at which the curves of different species turn upward, so that a form which has been developing in this direction during the last period only may have a shorter stem in its last instar than one in which this suture has been decreasing for a much longer period. To use a convenient analogy, some have run faster than others, some have had farther to go, and some began to run much earlier than others, the latter having won the race in the majority of cases.

Certain species, such as *Cirphis phragmitidicola*, apparently represent an incipient stage in this process of reduction, which, if it continues to operate progressively in the future, as it has in the past with other species, must result eventually in reducing the epicranial stem of this species to a fraction of its present length, a condition typified at present by the last instars of *Agrotis ypsilon* and *Feltia subgothica*.

To summarize the conclusion which we have thus far reached regarding the shortening of the epicranial stem in the postembryology of noctuid larvae: This process is a recapitulative one. It represents a secondary development occurring only in certain species with subterranean proclivities. It is of independent origin in different species, having begun at widely different times in race history. It is a progressive process, species in which it has begun continually undergoing greater reduction in the length of this suture. The intensity of this process has varied in different species, that is, it has gone on more rapidly in some species than in others.

In the following discussion, it will be shown that the rate of reduction in the length of the epicranial stem has been subject to an acceleration. The significance of the slopes and angles of both types of curves will now be considered. Certain of them turn upward at a smaller angle than others in the same period, indicating unequal rates of reduction in the stems of such species, as has been stated previously. A parallel situation may be seen in the left-hand portion of the curves, where some turn downward much more abruptly than others, showing that this primary lengthening process has also developed at very different rates according to the species. It should be

clearly borne in mind that these conclusions are based on a comparison of angles presented by different curves in the same horizontal unit. Such a comparison can be directly interpreted without danger of going astray, but in comparing the slopes of parts of the same curve or of portions of different curves in different units, we are confronted with a situation which is liable to be misleading without an understanding of the relation which these units bear to one another.

For the purpose of analyzing this relation let us suppose that a certain species has a larval life of sixty days, which we will divide without regard to stadia into six equal periods of ten days each. Suppose further that we represent the curve of this species as we have those in Plate I, using for units, however, these six equal periods instead of stadia. Now in this graphic representation, the periods in phylogeny to which these ten-day divisions correspond are given equal value, whereas in reality this is very far from true. According to the general conception of the working of the law of recapitulation, the first ten days would represent a much longer phylogenetic period than the second ten, which, in turn, would correspond to a portion of the race-history of much greater duration than would the third ten days, and so on until the last ten day division, whose corresponding phylogenetic period would be, perhaps, but a minute fraction of that of the first ten days. The fact that the change in the position of the setae of the trunk, a recapitulative one, is very much greater from first to second instars, than thruout the entire remainder of the larval life illustrates this principle. To represent graphically this condition it would be necessary to extend greatly the length of the first unit, lengthening the second one to a lesser extent, the third a still lesser amount, and so on. We have no means of knowing what the relative lengths of these units should be in order to render the slopes of different parts of this hypothetical curve exactly representative of the relative rates at which these changes in epicranial index have evolved during different phylogenetic periods. We merely know in which direction to apply this sort of correction.

Another means of correction may be applied to this hypothetical curve, by leaving the units equal, as they are in Plate I, but dividing the sixty day larval life into six unequal periods, which gradually increase in length from younger to older. The same result would be accomplished in this manner as by keeping the periods equal and altering the length of the units, in the manner just described. For mechanical reasons it has been necessary to use stadia for our units in Plate I. As already demonstrated the lengths of stadia generally do not present a gradual increase from younger to older in this family, but are often about equal, except for the last, which is usually much longer, and for the first, which is long in some species. The employment of stadia as units, then, offers no correction, except possibly for the last unit, where this stadium is long. It is question-

able whether or not this correction, brought about in consequence of the longer duration of the last larval stadium, where this condition is found, is sufficiently extensive to render significant a comparison of the slopes of the last two units without further correction. Possibly these two units may remain equal as they stand in Plate I, the long last stadium having taken care of the correction, which would otherwise have to be introduced by increasing the length of the next to last unit. Where we find a long first stadium we should perhaps increase the length of the first unit even more than otherwise. It is well to recall at this point, however, that the length of a stadium may not be an index to the amount of postembryonic development undergone during it, since, as has been previously suggested, the longer stadium may be correlated with a slower development. If this be true the long first stadium requires no greater correction than the shorter one.

When we compare different parts of the same curve, then, with reference to slope, it must be remembered that the units should not be of equal length, as they stand in Plate I, but that each should be somewhat longer than the one which follows it. The possibility that the last two units may need little or no alteration in order to represent the true condition should also be considered. Furthermore, the first unit may require greater lengthening than otherwise for species with a long first stadium, such as *Dipterygia scabriuscula*. The general effect of this correction is to make the primary curving downward on the left of the chart very gradual and to accentuate the secondary curving upward on the right. Upon applying this correction mentally to Plate I, we note that this secondary shortening of the epicranial stem has proceeded with much greater rapidity than its primary lengthening. It becomes evident, moreover, that this primary process has generally accelerated with the passing of time, altho the curves seem to indicate the opposite condition before the necessary correction is applied. Straight lines, where they occur on the uncorrected chart, do not indicate a constant rate of evolution, but an acceleration. The secondary shortening process has also progressed at an increasing rate, the acceleration being much greater than in the lengthening process.

The two species of the genus Phytometra examined present a distinct type of curve in which the epicranial index remains unchanged thruout the first two periods, followed by the usual accelerated lengthening. The epicranial stem of the last instar of these larvae is as short as that of the average species whose curve turns upward. This condition is evidently due to the fact that in this genus the primary lengthening has been delayed until the third period, so that the epicranial stem has not been evolving in this direction for a sufficiently long time to enable it to attain the length common to species in which this suture has not undergone secondary reduction.

This postembryological study has provided a source of evidence as to the evolution of habit within this family. The correlation between the reduced condition of the epicranial stem and the subterranean mode of life has already been discussed. We have seen that an anatomical relation exists between the short epicranial stem and the cephalic direction of the mandibles, this latter condition being apparently an adaptation for burrowing in the soil. The period in phylogeny in which the shortening of this suture began, as indicated by the curves in Plate I, is to be regarded, then, as the one in which this biological specialization took place. The point of turning upward in one of these curves represents, in other words, the origin of the subterranean habit in the race history of the species in question. It is apparent that this mode of life has originated independently at different times in the phylogeny of different species. Entomology furnishes numerous instances of such independent origin of the same biological specialization in various groups of insects. The aquatic and parasitic modes of life, as well as the leaf-mining and wood-boring habits exemplify this situation, the same habit having developed independently at different times in different groups.

We have demonstrated the accelerative nature of the secondary shortening of the epicranial stem. In the light of the established correlation between this structure and the subterranean habit, it becomes evident that species developing tendencies to enter the soil have gradually become more markedly subterranean at an increasing rate with the passing of time. From this it follows that those forms having developed this habit earliest in race-history must present the most pronounced subterranean mode of life at present. From the data we have collected it is clear that this is precisely the case. The species whose curves turn upward earliest in postembryology reveal the greatest degree of "subterraneanness," as evidenced by their resistance to submergence and other biological traits. Those forms which have been subterranean longest, in other words, are the most subterranean now. This point supports further the corollary that corresponding postembryological stages in different species represent the same phylogenetic period, inasmuch as the conclusions obtained on the basis of this corollary agree with the biological data regarding the relative "subterraneanness" of species.

It has been noted that certain species, typified by *Cirphis phragmitidicola* and *Ceramica picta*, appear to represent an incipient stage in the development of the subterranean mode of life, entering the soil only under extreme stress during the feeding period. The curves of such forms turn upward but slightly, in the last unit only. If the development of this habit continues progressively in the future as it evidently has in the past, such slightly subterranean species must eventually become markedly so, like *Agrotis ypsilon* or *Feltia subgothica*. This suggests the interesting possibility

that we may have in the remote future a larger number of species of subterranean noctuid larvae than at present. However speculative this proposition may seem, it is undoubtedly indicated by the data at hand.

When we compare subterranean and non-subterranean larvae with reference to the number of individuals parasitized, the advantage of the former mode of life becomes obvious. From more than a thousand individuals of *Feltia subgothica* reared during three successive years, but four or five have been infested with insect-parasites, whereas larvae remaining above ground during the daytime, such as the cabbage-looper or the army-worm, are frequently 90% parasitized by many insect-enemies. Subterranean cutworms are similarly free from attack by birds. Egg-parasites affect both classes equally. Fungi and wilt diseases seem to be as generally found in non-subterranean hosts as in those whose habitats are associated with the earth. The only nematodes thus far recorded from noctuid larvae were taken from a single subterranean cutworm, Agrotis sp., by the author. The apparent rarity of these parasites in cutworms indicates that they are not to be regarded as important enemies. Large carabid beetles are evidently the only important natural enemies affecting subterranean lepidopterous larvae to an appreciably greater extent than those which do not enter the soil. Yet these feed extensively upon larvae above ground, some even climbing trees in search of their prey. From the point of view of protection from natural enemies, the subterranean habit unquestionably offers important advantages, which probably accounts to a large extent for its progressive nature in the course of evolution.

The interpretation of certain exceptional curves in Plate I is problematical. That of *Agrotis clandestina* fails to turn upward, altho the larva of this species is to some extent subterranean. The primary lengthening of the epicranial stem of this species is but slight in the last period, indicating the retarding of this process, which must necessarily precede the secondary shortening. Not only does the curve thus indicate an incipient condition in the reduction of this suture, but the bright coloration of this cutworm points further to recent development of the subterranean habit. Cutworms which enter the soil generally tend either to lose their pigment, like *Sidemia devastatrix*, or to become indistinctly marked and dully colored. We know of few equally subterranean larvae with such bright colors and distinct markings as clandestina. *Agrotis c-nigrum*, to which this species is very closely related, exhibits similar but much less distinct markings and duller colors, its curve being typical of cutworms which burrow in the ground. Clandestina is probably one of our "youngest" cutworms, this habit, altho quite well developed, being too young phylogenetically to be accompanied by a marked shortening of the epicranial stem.

Catocala ? vidua presents the opposite situation, where we have an arboreal form whose curve turns upward slightly in the last unit. Possibly the larva of this species enters the soil to pupate, altho the members of this genus typically spin cocoons above the ground. The epicranial stem of the arboreal *Heterocampa bilineata* (Notodontidae) undergoes a marked secondary shortening, showing that this condition in families other than the Noctuidae is not necessarily associated with the subterranean mode of life. In spite of the marked turning upward in the curve for this species, the stem of the last instar is much longer than in larvae which enter the soil. The peculiar curve of the bag-worm bears some relation, perhaps, to its unusual feeding habit. A much more extensive postembryological study of this structure must be made, embracing many families of lepidopterous larvae, before we can hope to understand the significance of these changes.

Having discussed the postembryology of the epicranial stem and its biological significance, it now remains for us to consider the phylogenetic evidence which this study may afford. A certain degree of correlation between the types of curves in Plate I and taxonomic groups can be observed. Attention has already been directed to the peculiar type of curve presented solely by the two representatives of the Phytometrinae examined. Whether or not this type is characteristic for the entire subfamily we cannot state. When we consider the pronounced uniformity of the larvae of this group, however, it seems fairly probable that this is so. The species of Catocala represented exhibit an unusually great increase in the length of the epicranial stem during the first two periods. Species of the same genera have curves similar in position and shape, except where the secondary turning upward has interfered. This process, being associated with the subterranean habit, which often differs in closely related species, cannot be relied upon as an indication of phylogenetic relationship. With curves which turn upward the primary portions only can be safely compared from a taxonomic point of view. For instance, *Cirphis unipuncta* presents a typical non-subterranean type of curve, whereas those of *phragmitidicola* and *pseudargyria*, which are very closely related to this species, are of the incipient subterranean type. The difference in the later postembryonic development of this suture in *Agrotis c-nigrum* and *clandestina* has already been referred to. A comprehensive series of such curves would unquestionably afford valuable phylogenetic information.

All of the species examined were established earlier than the first phylogenetic period represented in Plate I. In other words, none of the curves of closely related species have started from the same point in the first unit. A more extensive series might very possibly discover species so recent that their curves would unite in a common line in the first one or two units.

The race-history of the reduced epicranial stem may be represented by the diagram shown in figure 61, which indicates both the independent origin and progressive nature of this condition. In this figure 1 represents the persistence of the long-stemmed ancestral condition to the present. A form which has departed relatively recently from the condition of 1 and which tends toward the development of a shorter stem is illustrated by 2. The most ancient departure from 1 is represented by 6, which reveals the shortest epicranial stem at present. The conspicuousness and apparently fundamental nature of this character would tempt taxonomists to employ it for the division of larger groups within this family. Our knowledge of its phylogeny, however, derived from this postembryological study limits its taxonomic use to the separating of species and in some cases, perhaps, of genera. The taxonomist studying this structure without regard to postembryological evidence, but drawing his conclusions entirely from the comparative morphology of the last instar, would, in all probability, be misled as to its phylogeny. He would, of course, without the aid of postembryology correctly conclude that the short stem represented a specialized condition but, on the other hand, no clue as to the independent origin of the shortening of this suture would be afforded him. Working on this basis, he would most naturally be led to believe that the species with the short epicranial stem represented, at least for the most part, a phylogenetic unit. The fact that this condition is often found in closely related genera would add to this impression. Its independent origin in different species in the same subfamily or genus could not possibly be deduced without a postembryological study. Figure 60 represents diagrammatically the erroneous interpretation of the evolution of the short epicranial stem, which would be most naturally derived from a study confined to full-grown larvae. In this diagram 1 represents the persistence of the primitive long-stemmed condition, as in Figure 61. The short-stemmed condition, on the other hand, is shown as descending from a common ancestor. The preservation of the condition of the most ancient departure from 1 is illustrated by 2, whereas in reality the condition of 2 is the most recent departure in this direction. According to Figure 60, 6 has developed most recently and reveals the most extreme specialization. In reality the condition of 6 at the present time is found in species in which this tendency appeared earliest in phylogeny, as shown by Figure 61. A comparison of these two diagrams, the correct and the false, derived respectively with and without regard to postembryology, demonstrates in a convincing manner the phylogenetic value of this neglected source of evidence.

POSTEMBRYOLOGY OF LABIUM AND SPINNERET

The most profound postembryonic changes undergone by noctuid larvae are those in the form of the spinneret, while other parts of the labium

also present considerable difference according to the instar. The stipular setae frequently increase in relative size during larval life (Figs. 40, 43, 44), altho they may remain about the same (Figs. 33, 38). A striking decrease in relative size is always undergone by the two sensoria of the palpiger and by the pair of smaller ones on the proximal semicircular sclerite of the spinneret (Figs. 29-32, 33-36, 38, 40, 41, 43-45). As previously mentioned the same situation is presented by those of the head, altho not so marked. This appears to be a non-recapitulative change due to the mechanics of growth. The pronounced decrease in the relative size of the ocellarae already discussed offers an apparently parallel situation. It seems evident that the modified hypodermis of sensory organs, whether of visual or of chemical sense, grows more slowly than the ordinary hypodermis.

In the first instar of some species the proximal sclerite of the spinneret is continuous between the sensoria, forming a complete ring instead of a semicircle, as it sometimes does in the older noctuid larvae (Figs. 33-38). The fact that the former condition is of quite frequent occurrence thruout the order suggests that it may be the primitive one, in which case this change is to be regarded as a recapitulation, the semicircular sclerite of the noctuid larva representing the remnant of a complete ring. The first instars of *Polia renigera* and of *Agrotis ypsilon*, on the other hand, exhibit the condition typical of fully grown noctuid larvae with respect to this point (Figs. 29-40). In the former species, however, a secondary chitinization appears in the last instar, connecting the two ends of the semicircle (Figs. 31-32).

The palpi undergo changes in form and in the shape and relative size of their setae. A comparison of Figures 30 and 31, 33 and 38, and 40 and 44 reveals the fact that both segments of the palpus become relatively longer and narrower during development. Since there appears to be no evidence indicating whether or not the ancestral palpus was shorter and broader than the typical one of existing forms, we cannot attempt to classify this change. The significance of the striking reduction of the seta of the proximal segment during larval growth is also problematical. Usually, altho not always, the terminal seta of the distal segment becomes much more slender and relatively shorter in the later stadia. *Lycophotia margaritosa* appears to present an exceptional situation in the development of all of the setae of this region. Those of the stipula fail to increase in relative size as they usually do and the terminal one of the palpus becomes relatively larger in the course of growth, whereas the reverse is typically true. The reduction of the terminal seta commonly found in the Noctuidae is paralleled in certain leaf-miners figured by Trägardh. Moreover, the terminal setae of the antennae and maxillae of caterpillars are frequently short and stout in the first instar, becoming normal in form during development. The significance of these changes cannot be definitely determined in

the present state of our knowledge of their phylogeny. They are probably non-recapitulative but are evidently not to be explained by the mechanics of growth, since exceptional instances occur.

It was mentioned in the morphological part of this paper that the seta of the proximal segment of the palpus presents a specialized condition with reference to position in *Lycophotia margaritosa*, where it is located mesad instead of laterad of the small terminal segment (Fig. 38), a very exceptional situation. The location of this seta is normal in the first instar (Fig. 33), the unusual position found in the later instars being the result of its migration around the cephalic side of the distal segment. This process is unquestionably a recapitulation.

The postembryology of the spinneret of noctuid larvae is a highly complicated and most interesting subject. Four distinct types of development of this structure have been observed and most probably a more extensive study will reveal the existence of a number of additional ones in the order. In Type I the spinnerets of both first and last instars are subequal in length and distinctly longer than in the intermediate stadia. The species of Phytometra examined present this condition. Type II is represented by *Lycophotia margaritosa*. The spinneret of the first instar of this species (Fig. 34) is much longer than the palpi and fairly slender, the condition most frequently found in the fully grown larvae thruout the family. In the second stadium it is very much shorter and reveals slight projections on both upper and lower distal margins (Figs. 35, 36). The reduction in length proceeds a little further in the third instar and the distal projections become longer (Fig. 37). Moreover the lateral emarginations, which are very rudimentary in the first two stadia, are fairly deep in this one, so that the upper and lower lips, previously described, become evident. From this stadium to the last there is no appreciable change in relative length, but the projections gradually become elongated on both lips, forming a well developed fringe, and the proximal fold and its sclerite decrease considerably in relative width. The lower lip shows a tendency to become bilobed. The decrease in the relative size of the sensoria has already been discussed. *Polia renigera* exemplifies Type III. The spinneret of the first instar is somewhat shorter than the palpus (Figs. 29, 30). In the following stadia a gradual increase in its relative length occurs and the proximal fold becomes markedly elongated on the cephalic aspect. The condition in the fully grown larva is shown in Figures 31 and 32, where the spinning organ is somewhat longer than the palpi and the extension of the proximal fold reaches about half way to its distal end. The secondary chitinization of the spinneret and of the proximal fold, like that between the sensoria of the proximal sclerite, does not appear until the last instar. Type IV presents very little change in the relative length of the spinneret in different instars, as may be seen by comparing Figures 40, 41, 43, and 44, representing the

postembryology of the spinneret of *Agrotis ypsilon*, which typifies this type of development. The proximal sclerite descreases in relative width as in the other types. The fold in this species increases as it does in *Polia renigera* but to a much lesser extent. A secondary chitinization appears on the fold continuous with the primary sclerite but of a lighter color, again recalling the somewhat similar condition in *renigera*. The fringe develops much as in *Lycophotia margaritosa*, its first indication appearing as slight rounded projections on the upper lip of the second instar (Fig. 42). Unlike *margaritosa*, however, the lateral emarginations are well developed in this stadium and the distal projections appear only on the upper lip. In the following instars the lower lip becomes distinctly bilobed and a small fringe, which presents considerable individual variation, develops on the upper one from the projections which appear first in the second instar (Figs. 43-46).

The essential basis for the recognition of these four types is the difference in the relative length of the spinneret in different stadia. The other changes described will be considered later. In Type I the spinneret is longer in the first and last instars than in the others; in II it is long in the first stadium, becoming short in the course of development; the condition in III is exactly the opposite, the first instar having a short spinneret which develops into a long one; in IV it is short thruout all stadia. Each of these types of postembryonic development of this structure is correlated with a different distribution of the spinning habit with reference to the instars. The species falling under Type I, long in first and last stadia, spin threads in the first instar and a well developed cocoon in the last. In Type II, long to short, the first instar only spins silk, the cocoon-spinning habit having been entirely lost in correlation with subterranean pupation. Type IV, short thruout, has lost the spinning power in all stadia.

These changes in the relative length of the spinneret during postembryonic development are obviously to be explained by the unequal function of this structure in different stadia rather than by recapitulation. Inasmuch as the ancestral noctuid larva had a long, slender spinneret, as has been shown on the basis of morphological evidence, the expression of the recapitulative force would result in a relative shortening of this organ from first to last instars in those forms where the spinneret of the last stadium has been reduced. Whereas this condition is found in Type II, where the first instar spins silk and the last one does not, it fails to occur in IV, where the spinneret is short in all stadia, the spinning habit being absent thruout. Similarly species which have preserved the long ancestral spinneret in the last stadium would exhibit this condition in all instars, if recapitulation were the only factor operating, whereas marked inequality in the relative length of this organ in the different stadia is found in both Types I and III, where the spinneret is long in the last instar. This situation exemplifies

what may prove to be a general zoological law, namely, *When the expression of the recapitulative law conflicts with the development in successive instars of a series of adaptations to different functions, or to different degrees of the same function, the latter is dominant* .

In species where either all or none of the instars spin silk it might be argued that the recapitulative force would be allowed to express itself, since the factor of unequal function would be eliminated. Instances are rare in the Noctuidae where the larvae of all stadia spin silk in approximately proportionally equal amounts, as in the tent-caterpillar, *Malacosoma americana*. *Sidemia devastatrix* furnishes the only instance known in the Noctuidae where this habit appears to be equally developed thruout larval life, and the data in this case are not conclusive, since live larvae of only the first and last three stadia have been seen by the author. The first instar spins silk threads during the feeding period, the fourth and fifth form slight cocoons in which to molt and the last pupates within a cocoon. Since the long ancestral spinneret has been preserved in this species, the expression of recapitulation would not involve any postembryonic change and so far as known none occurs, the spinneret of all stadia examined being long. Type IV presents the opposite condition where there is no silk-spinning in any stadium. In this type the recapitulative law is not followed with respect to the relative length of the spinneret, which remains approximately the same thruout larval development.

An analysis of the possibilities with regard to the original use of the habit of spinning silk in the order and in the family reveals the fact that we cannot reasonably expect to encounter an expression of the recapitulative force in species where the factor of unequal function has been secondarily eliminated, as it has in Type IV. There are at least three ways in which this habit may have originated in the ancestral lepidopterous larva. It may have developed originally in the first instar, functioning as a means of dissemination by the wind, as it does in various existing species, or in some other capacity. Apparently better grounded is the hypothesis that the spinning of a cocoon by the fully grown larva represents the primitive condition, the other instars having in certain forms subsequently developed the habit of spinning threads. Perhaps most probable of all is the possibility that this habit was originally equally developed in all stadia, as it is now found in the case-bearers, tent caterpillars, borers which line their burrows and miners which line their mines with silk. The frequent occurrence of this condition among larvae of the more generalized families lends weight to this view, altho the limitation of the spinning of silk to cocoon-spinning often met with thruout the order favors the conclusion that this situation is the ancestral one.

However this may be, the very exceptional occurrence among noctuid larvae of the equal development of the silk-spinning habit in all stadia

strongly indicates that the spinneret functioned unequally in different instars in the primitive caterpillar of the family. The spinning of silk most probably occurred in the last instar or in both first and last, these two conditions being the only ones of general occurrence in forms which retain the primitive long spinneret in the fully grown larva. Thus the factor of unequal function in the postembryology of the spinneret of noctuid larvae is most probably an ancestral one. In Type IV this factor has become secondarily eliminated by the loss of the power to spin silk in both first and last instars. We cannot reasonably expect, therefore, that recapitulation would find expression in the postembryology of this type with respect to the relative length of the spinneret.

As previously concluded in the treatment of the morphology of the spinneret the fringe is a specialization which has developed in correlation with the habit of subterranean pupation, apparently functioning as a brush for the lining of the earthen cell with a secretion of the silk-glands. The fact that it is well developed only in the last instar also supports this conclusion. The four types of the development of the spinneret just discussed are based only on its relative length and do not apply to the fringe, which often appears in both Types II and IV where the reduced spinneret occurs in the last instar. The appearance of the fringe in postembryonic development apparently represents a recapitulation. Since it functions only in the last instar, however, the factor of unequal functions has operated in the same direction as the recapitulative force, so that this process is not the expression of recapitulation alone. It falls under the same group in our classification of postembryonic changes as the development of the adfrontal suture, recapitulative and adaptive to unequal function.

The appearance of the lateral emarginations, which are present only in the reduced type of spinneret, have presumably developed in phylogeny as they do in postembryology. Since the upper and lower lips thus formed probably have to do with the function of the spinneret, which is performed only in the last instar, unequal function as well as recapitulation has operated in the production of this postembryonic change.

The appearance of the elongated proximal fold and of the secondary chitinization in the postembryonic development of *Polia renigera* (Figs. 29, 32) also recapitulates the phylogeny. Since these structures serve as a support for the spinneret, which is functional only in the last instar, unequal function also plays its part in these changes, which are evidently to be regarded as recapitulative and adaptive to unequal function.

The reduction in the relative width of the proximal sclerite is apparently of general occurrence within the family, this process always manifesting itself regardless of the trends of development along other lines. Until more definite knowledge is gained of the phylogeny of this sclerite no definite conclusion can be reached as to the significance of its reduction in relative

width during larval life. The same may be said of the loss of the portion of the proximal sclerite which lies between the sensoria in the first instar of *Lycophotia margaritosa*. Since morphological evidence indicates that both the palpiger and the proximal sclerite of the spinneret in noctuid larvae represent the remnants of a more general chitinization, it seems probable that both of these changes are recapitulative.

The taxonomic importance of the structure of the spinneret of the last instar has already been emphasized. It is obvious that the condition of this structure in the first instar also provides valuable phylogenetic information. In *Lycophotia margaritosa* and *Agrotis ypsilon*, where the spinneret of the last instar is essentially of the same type, that of the newly hatched larva is strikingly different. These two species are both of the subfamily Agrotinae. The habit of spinning threads in the first stadium, nevertheless, is apparently a comparatively fundamental one, hence the extent of the development of the spinneret in this stage, which is correlated with this habit promises to serve as a fundamental guide to relationships. It is important, therefore, that all accounts of the development of caterpillars state the situation with regard to the form of this organ and with reference to the spinning of threads in all instars. On the basis of the limited amount of data available as to the occurrence of silk-spinning in the first instar of noctuid larvae no correlation with the mode of life is apparent.

LARVAPODS

In the morphological discussion of the larvapods it was noted that the ancestral condition, where the four median pairs are well-developed, has been retained in the majority of noctuid larvae, altho in certain subfamilies the first one or two pairs tend to become reduced and are sometimes lacking. The incipient condition in the development of this specialization is exemplified by many Agrotinae, where the first two pairs are distinctly, altho not strikingly shorter than the others. In Catocala a more advanced condition is found, the first two pairs of larvapods being much smaller than the others. This process has proceeded still further in the specialized subfamily Hypeninae, where the first pair is without crochets or wanting altogether. The most specialized situation with respect to this process is exhibited by nearly all Phytometrinae, whose adults are undoubtedly among the most specialized noctuids, and by certain Catocalinae, such as Caenurgia, where the larvapods of only the fifth and sixth adbominal and of the anal segments remain.

If the postembryonic development of the larvapods were to recapitulate their phylogeny, we should expect to find a relative decrease in the size of the first one or two pairs from the first to the last instars in forms where these larvapods are reduced in size in the fully grown larva. In species where the last instar lacks the first one or two pairs they would be found,

at least in a vestigial condition, in the newly hatched larvae, unless their loss took place sufficiently early in phylogeny to restrict their appearance in ontogeny to embryonic stages. Since these two pairs of larvapods are generally present in the Catocalinae, their absence being rather exceptional, and since Hampson has reported them present in one genus of the Phytometrinae, this latter possibility must be regarded as highly improbable.

A study of the postembryology of these appendages reveals the fact that these hypothetical changes based on recapitulation alone are not found and that the reverse condition usually presents itself. Instead of becoming relatively smaller during the course of development, the first two pairs of larvapods typically increase in relative size from the first to the last stadia. Moreover, where they are wanting in the fully grown larva, no trace of them is found in the first instar. On the contrary, in certain genera of Agrotinae, Hadeninae, and Acronyctinae, the first pair is absolutely wanting in the first and second stadia, appearing in the third as a minute vestige and increasing in relative size thereafter. This condition is diametrically opposite to the one which would result from an expression of recapitulation. From these facts it may be stated conclusively that the appearance or the increase in the relative size of the first one or two pairs of larvapods in the postembryonic development of noctuid larvae are non-recapitulative changes, the effects of recapitulation having been completely obscured by other factors.

The reduction or absence in lepidopterous larvae of the cephalic one, two or three pairs of larvapods is correlated with the peculiar biological characteristic of walking with a looping gait. Noctuid larvae with this gait have been referred to as semi-loopers as opposed to the loopers of the Geometridae, where this gait is even more pronounced, since but one pair of median larvapods persists in the larvae of this family. Caterpillars of this type, because of the longer steps which they are able to take, can travel more rapidly for the amount of energy expended than those which walk in the usual manner. It is a matter of simple mechanics that the looping gait is the more efficient from the point of view of rapid progress. Loopers appear to be generally more active than other caterpillars, altho certain arctiids whose aptitude for traveling at a high rate of speed is frequently displayed, furnish an exception to this rule.

The evolution of this habit in the larvae of the Catocalinae, Phytometrinae, and Hypeninae is very probably to be accounted for by the advantage of rapid locomotion which is thereby undoubtedly gained. The looping gait enables these caterpillars to withdraw from undesirable situations with the minimum loss of time and with the minimum amount of exposure to the attack of enemies. When dislodged from the trees or the plants upon which they feed, usually in more or less protected situations, or, in the case of most Catocalinae, from the twigs upon which they rest, in

which situation they are protectively colored, those which can most rapidly regain a favorable environment must survive natural selection in the course of evolution. The many advantages gained by the power of rapid locomotion are so obvious that a detailed discussion of them would be superfluous.

Larvae of the ground and subterranean strata enjoy protection in a large measure by virtue of their nocturnal and subterranean habits. The proximity of their food to the ground, moreover, requires but little climbing for them to reach it. In the older comparatively inactive larvae of such forms the reduction of the first two pairs of uropods is generally not pronounced. *Caenurgia erechtea* and certain phytometrids afford exceptions to this rule. The occupation of the field stratum by the former species is very unusual for larvae of the Catocalinae and is, therefore, to be regarded as a biological specialization. The loss of the larvapods very possibly took place in the ancestor of this species previous to its migration from the tree to the ground stratum. However, this may be, the looping habit in noctuid larvae appears to be generally correlated with a relatively active mode of life and with one which often renders rapid locomotion especially advantageous. It is never found among the cutworms or their biological allies, except in the earlier stadia, being usually confined to the first two. These instars are semiloopers in the family in all instances known to the author, regardless of the gait of the older larvae. In the earlier stadia the larvae are markedly more active than in the later ones. The small size and proportionately long setae of newly hatched caterpillars render them decidedly subject to conveyance by the wind, a matter of common observation. This fact necessitates that they be generally more active than the older instars. Moreover, the large number of individuals hatching simultaneously from a single egg-mass demands dissemination either by the wind or by locomotion, considerable activity being involved in either case. The threads frequently spun only by the first instar serve as veritable parachutes in some instances and as anchors by which they attach themselves to the food-plant in others. The former employment of the thread, however, has not been actually observed in the Noctuidae, so far as known, altho it has been reported in other families and most probably occurs in this one. The apparently universal presence of the looping gait in young noctuid larvae, which is characteristic of the last instars of only the more active larvae of the family, such as the catocalas, is not at all surprising when we consider the especial need for rapid locomotion during the first one or two stadia.

The appearance or increase in the relative size of the first one or two pairs of larvapods during the postembryonic development of noctuid larvae is obviously the expression of the unequal function of these structures in different stadia. The extent of the reduction of these larvapods is proportional to the extent of the development of the looping gait, which is correlated with the amount of advantage gained by greater or less rapidity in

locomotion, an advantage which is greater in the earlier instars than in the later, especially with noctuid larvae of the ground and subterranean strata. This factor of unequal function in different instars has completely obscured the effects of recapitulation, as in the parallel situation of the unequal function of the spinneret, which has been previously discussed. Thus additional support is given to the law stated to the effect than unequal function is dominant over recapitulation when these factors act in opposition to one another.

Henneguy states that the gaining of the first pair of larvapods occurs during postembryonic development in the European noctuids, *Agrotis pronuba*, (Agrotinae), *Polia nebulosa* (Hadeninae) and *Trachea atriplicis* (Acronyctinae). This condition has been found by the author in *Agrotis ypsilon* and in *Feltia subgothica*, altho the first pair of larvapods is fairly well developed in the first instars of *Agrotis c-nigrum* and *badinodis*. In *Lycophotia margaritosa*, of the same subfamily, they are present but extremely vestigial, bearing only two or three crochets. A similar difference with respect to this point is also found in the genus Polia. The American *renigera* has the first pair of larvapods comparatively well developed in the first stadium, as does the rather closely related *Ceramica picta*, whereas they are reported absent in the European *Polia nebulosa*. In like manner they are not strikingly smaller than the second pair in the newly hatched larvae of *Sidemia devastatrix*, altho Henneguy states that they are absent in those of the closely related *Trachea atriplicis*.

The difference in the development of the first pair of larvapods in closely related species indicates that this developmental character is not a fundamental one from the taxonomic point of view. The scattered occurrence of their absence in the first two stadia thruout the subfamilies Agrotinae, Hadeninae, and Acronyctinae shows that this condition, like the length of the epicranial stem and like the number of molts, has originated independently in different species. The tendency toward the reduction of the first two pairs of larvapods is, however, general thruout the family.

In the first instars of *Catocala illia*, *amatrix*, *innubens*, *cara*, and of *Homoptera lunata* the first two pairs are no more reduced than in the other subfamilies mentioned, altho the fully grown larvae of the Catocalinae are typically characterized by the very small size of the first two pairs of larvapods compared to the others. The tendency toward their marked reduction in this subfamily evidently applies to all stadia, rather than to the early ones alone, altho this process has advanced somewhat further in the young larvae than in the old ones, as it generally has throughout the family. The lack of striking difference between the relative size of the first two pairs of larvapods of the early instars and those of the later ones is a fundamental developmental character, which is evidently correlated with the active mode of life of the fully grown larvae of this subfamily.

CROCHETS

During the growth of noctuid larvae the number of crochets increases markedly on all of the larvapods. This process in *Agrotis ypsilon* may serve as a typical example. The formula for the first instar is -, 3, 5, 7, 8, the first pair of larvapods being absent, for the second it is -, 5, 7, 7, 8, for the third 3, 7, 9, 10, 14, for the fourth 9, 13, 13, 13, 16, for the fifth 12, 13, 15, 16, 19, for the sixth 16, 18, 19, 19, 20, and for the fully grown larva it is 16, 20, 20, 21, 25. Like the ocellarae and the sensoria the crochets are relatively much larger in the earlier than in the later stadia. Consequently there is sufficient space on the larvapods of the first instar to accommodate but relatively few crochets. A survey of the number found in the larvae of the more generalized families in the order, as well as in caterpillars generally, offers absolutely no evidence favoring the view that this change is recapitulative. The increase in the number of crochets is apparently to be accounted for by the mechanics of growth.

Generally throughout the order the larvapods whose distal ends have the greater diameter bear the larger number of crochets. This relation is also clearly revealed by the condition found in an individual larva whose different pairs of larvapods differ in size. Since, in such an individual, the crochets are of approximately the same size on both large and reduced larvapods, there is naturally a larger number of them on the former. Hence with the increase in the relative size of the first two pairs, previously discussed, the number of crochets increases proportionally. But this change in the relative size of the larvapods is due to unequal function, as already determined. Therefore, the increase in the number of the crochets on the first two pairs is unquestionably the expression of two factors, the mechanics of growth and unequal function. This change is, therefore, to be classified as mechanical-adaptive.

The analogous process on the other pairs is, on the other hand, not influenced by the adaptive factor, since there is no appreciable change in the relative size of these larvapods during larval growth. Hence the mechanics of growth alone is responsible for this change. The fact that the increase in the number of the crochets of the first two pairs is considerably greater than that of the others is consistent with the compound nature of the former postembryonic change as opposed to the simple one of the latter.

SUMMARY

The principal results yielded by this investigation of the postembryology of noctuid larvae may be summarized as follows:

(1) The number of molts is characteristic of species, altho influenced to some extent by external factors.

(2) The largest number of molts, the greatest amount of larval growth, and the highest fecundity are three mechanically correlated conditions.

(3) These three conditions represent a specialization, the larger number of molts and higher fecundity having been derived from the smaller number, which is correlated with lower fecundity.

(4) The conditions of larval growth, number of molts, and higher fecundity have arisen independently in different species.

(5) An investigation of the postembryonic development of all external structures of noctuid larvae has revealed the existence of many previously undescribed changes.

(6) Three factors have been identified as operating in the production of the changes observed, recapitulation, adaptation to unequal function in different stadia, and the mechanics of growth.

(7) These factors may express themselves singly or in various combinations, in which case they may operate either in the same direction or in opposition to one another.

(8) Recapitulation is essentially different from the other two factors in that it is the expression of a general law, which fails to manifest itself only when its effects are obscured by those of other factors.

(9) When recapitulation and adaptation to unequal function conflict, the latter is dominant.

(10) When the factor of unequal function becomes secondarily eliminated, the recapitulative force remains unexpressed.

(11) The postembryonic changes found have been classified according to the factor or combination of factors responsible for them. This classification is as follows:

(I) Recapitulative.—Changes in the relative length of the epicranial stem, in the extension mesad of the postgenae, and in the depth of the labral cleft; the migration ventrad of the occipital setae, of the head setae v1, v2, and probably f1; changes in the coloration of the head and body, in the sculpturing of the cuticle, in the location of the body-setae, except those of the first two pairs of larvapods, and in the form of the mandibles; the reduction of the primary chitinization and acquisition of secondary chitin-

ization in the proximal sclerite of the spinneret; the migration mesad of the proximal seta of the labial palpus in Lycophotia; the secondary appearance of the tubercle of the seta rho in certain phytometrids.

(II) Non-recapitulative.—(a) Adaptive to unequal function in different stadia.—Changes in the form of the setae of the head and trunk and in the relative length of the spinneret; the acquisition of the first pair of larvapods; the increase in the relative size of the first two pairs of larvapods; changes in the position of the setae of these larvapods. (b) Due to the mechanics of growth.—The decrease in the relative size of the head, ocellarae, and sensoria; the migration ventrad of the head-setae v2, v4, and v5; the increase in the number of the crochets of the larvapods of the fifth and sixth abdominal segments.

(III) Compound, (a) recapitulative-adaptive.—The appearance of the adfrontal sutures; of the fringe, lips, and secondary chitinization of the spinneret; the elongation of the proximal fold of the spinneret. Compound, (b) adaptive-mechanical.—The increase in the number of crochets of the first two pairs of larvapods.

(IV) Problematical.—Changes in the form of the antennae, in the relative size of the setae of the stipula, and in the form of the labial palpi; the reduction of the setae of the labial palpi and antennae; the loss of the tubercles of the body-setae.

(12) The great value of a comparative postembryological study of species as a source of phylogenetic information has been demonstrated, chiefly by means of a detailed investigation of the development of the epicranial stem.

(13) Different types of postembryonic development of various structures, especially of the spinneret, epicranial stem, and larvapods, furnish developmental characters of considerable taxonomic importance. The condition of these structures should be given in detail in all descriptions of young caterpillars. The relative length of the spinneret of the first instar is especially important. The postembryonic development of the epicranial index offers an excellent means of determining relationships.

(14) Various correlations between structural and biological postembryonic changes have been established, such as those between the relative length of the spinneret and the amount of silk spun in different stadia, between the development of the fringe of the spinneret and the habit of subterranean pupation, and between the acquisition or relative increase in size of the first pair of larvapods and the decrease in general activity.

(15) The correlation between the subterranean mode of life, the resistance to submergence in water, and the short epicranial stem has been demonstrated. By virtue of this relation the postembryology of the epicranial stem has revealed the progressive nature and independent origin of the subterranean habit of noctuid larvae.

(16) The significance of the adfrontal suture has been determined upon the basis of postembryological evidence. This suture is a modification functioning as a means of ecdysis at the time of pupation.

(17) Sensory hypodermis, such as that of the ocellarae and sensoria, does not grow as rapidly as the ordinary hypodermis.

POSTSCRIPT

Much of the data of this investigation is included in twelve statistical tables which were submitted with the manuscript. The intricacy of these tables is such that it has been impossible to reproduce them here. They were included in the original copy of the thesis which is deposited in the Library of the University of Illinois, where they can be consulted by those interested.

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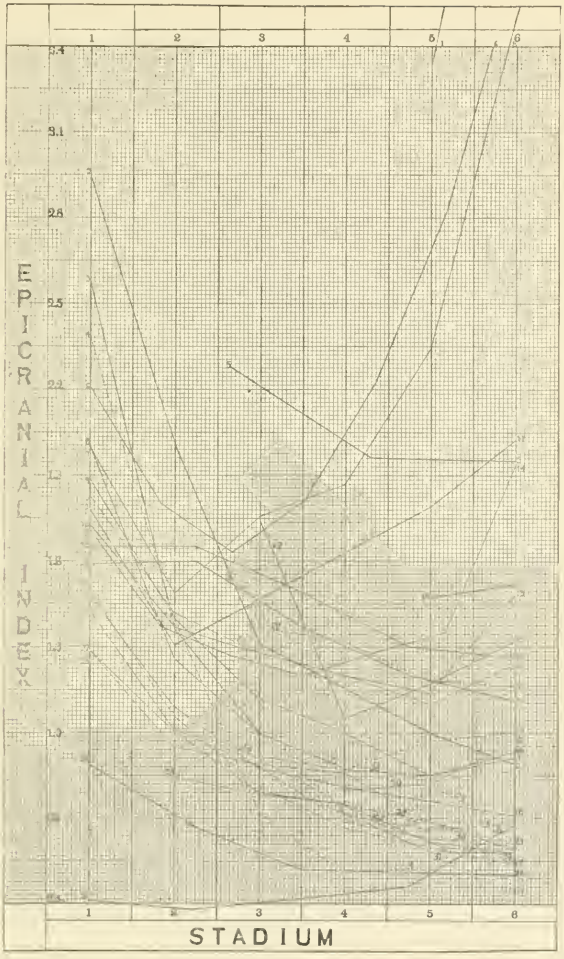
PLATE I

EXPLANATION OF PLATE I

POSTEMBRYOLOGY OF THE EPICRANIAL STEM

GRAPHIC REPRESENTATION OF THE EPICRANIAL INDEX.
EACH SPECIES REPRESENTED BY A CURVE

1. *Feltia gladioria* (Noctuidae).
2. *Conistra* sp. (Noctuidae).
3. *Catocala amatrix* (Noctuidae).
4. *Catocala ?vidua* (Noctuidae).
5. *Vitula edmansii* (Pyralidae).
6. *Agrotis ypsilon* (Noctuidae).
7. *Catocala cara* (Noctuidae).
8. *Feltia subgothica* (Noctuidae).
9. *Ceramica picta* (Noctuidae).
10. *Agrotis c-nigrum* (Noctuidae).
11. *Sidemia devastatrix* (Noctuidae).
12. *Polia meditata* (Noctuidae).
13. *Polia renigera* (Noctuidae).
14. *Lycophotia margaritosa* (Noctuidae).
15. *Phytometra biloba* (Noctuidae).
16. *Phytometra brassicae* (Noctuidae).
17. *Catocala* sp. (Noctuidae).
18. *Dipterygia scabriuscula* (Noctuidae).
19. *Prodenia ornithogalli* (Noctuidae).
20. *Cirphis unipuncta* (Noctuidae).
21. *Agrotis clandestina* (Noctuidae).
22. *Caenurgia erechtea* (Noctuidae).
23. *Homoptera lunata* (Noctuidae).
24. *Nephelodes emmedonia* (Noctuidae).
25. *Thyridopteryx ephemeraeformis* (Psychidae).
26. *Cirphis ?pseudargyria* (Noctuidae).
27. *Hemerocampa leucostigma* (Liparidae).
28. *Papaipema nebris* (Noctuidae).
29. *Epizeuxis lubricolis* (Noctuidae).
30. *Laphrygma frugiperda* (Noctuidae).
31. *Homoptera lunifera* (Noctuidae).
32. *Cirphis phragmitidicola* (Noctuidae).
33. *Heterocampa bilineota* (Notodontidae).



RIPLEY, NOCTUID LARVAE PLATE I

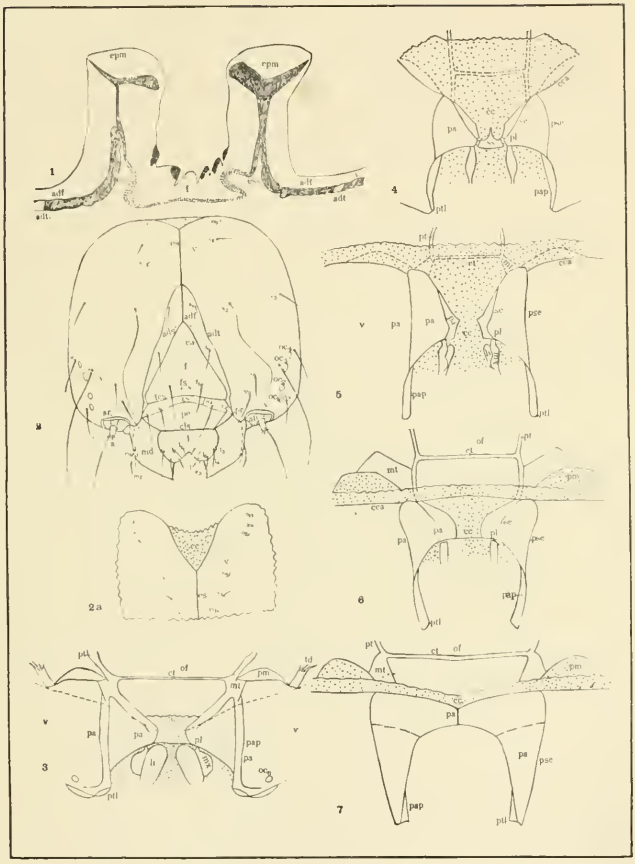
PLATE II

EXPLANATION OF PLATE II

EPICRANIAL STEM AND TENTORIUM

1. *Cirphis unipuncta*, last instar, transverse section thru front and adfrontals, soft parts removed by potash.
2. *Cirphis unipuncta*, last instar, cephalic aspect of head.
2a. *Cirphis unipuncta*, last instar, dorsal portion of vertex and cervacoria.
3 *Zeuzera pyrina* (Cossidae), last instar, postgenal region, ental aspect.
4. A pyralid, last instar, postgenal region, ectal aspect.
5. *Cacoecia* sp. (Tortricidae), last instar, postgenal region, ectal aspect.
6. *Thyridopteryx ephemeraeformis* (Psychidae), young larva, postgenal region, ectal aspect.
7. *Thyridopteryx ephemeraeformis*, last instar, postgenal region, ectal aspect.

a antenna
adf adfrontal sclerite
adt adfrontal suture
an antacoria
cc cervacoria
cca attachment of cervacoria
ccc chitinized cervacoria
cls clypeo-labral suture
cs clypeal suture
ct corpotentorium
ea epicranial arm
epm epicranial parademe
es epicranial stem
ess epicranial suture
f front
fcs fronto-clypeal suture
fs frontal sensorium
l labrum
li labium
mi-2 mandibular setae
md mandible
mt metatentorium
mx maxilla
ol-3 occipital setae
ocl-6 ocellarae
of occipital foramen
pa postgena
pap postgenal parademe
pe preclypeus
pl paracoila
pm parademe
pr precoila
pse secondary postgenal suture
pt pretentorium
ptl postcoila
se secondary of suture
svl-3 sensoria vertex
v vertex
vl-9 setae of vertex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1
adf
alf
adt
4
ec
ps
pa
pl
pap
ptl
5
pse
6
mt
7
2a
3
pap
ptl

PLATE III

EXPLANATION OF PLATE III

CAUDAL ASPECT OF HEAD, TENTORIUM, POSTGENA

8. *Epargyreus tityrus* (Hesperiidae), last instar, postgenal region, ectal aspect.
9. *Cirphis unipuncta*, last instar, caudal aspect of head.
10. *Polia renigera*, last instar, postgenal region, ectal aspect.
11. *Nephelodes emmedonia*, last instar, postgenal region, ectal aspect.
12. *Feltia subgothica*, last instar, postgenal region, ectal aspect.
13. *Cirphis unipuncta*, last instar, cephalic aspect of head, ental surface.
14. *Cirphis unipuncta*, last instar, caudal aspect of head, ental surface.

a antenna
ar antennaria
cc cervacoria
cca attachment of cervacoria
ccc chitinized cervacoria
ct corpotentorium
epm epicranial parademe
ex epipharynx
mt metatentorium
ocl-6 ocellarae
f occipital foramen
pa postgena
pap postgenal parademe
pas postgenal sensorium
pl paracoila
pm parademe
pox postpharynx
pr precoila
pse secondary postgenal suture
pt pretentorium
ptl postcoila
se secondary suture
td tendon
tm torma
vl–13 setae of vertex

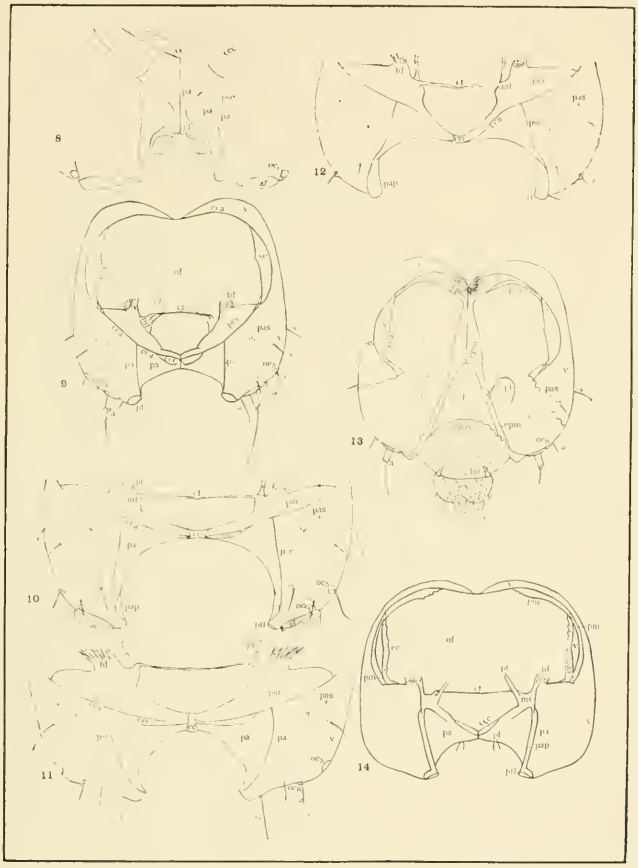


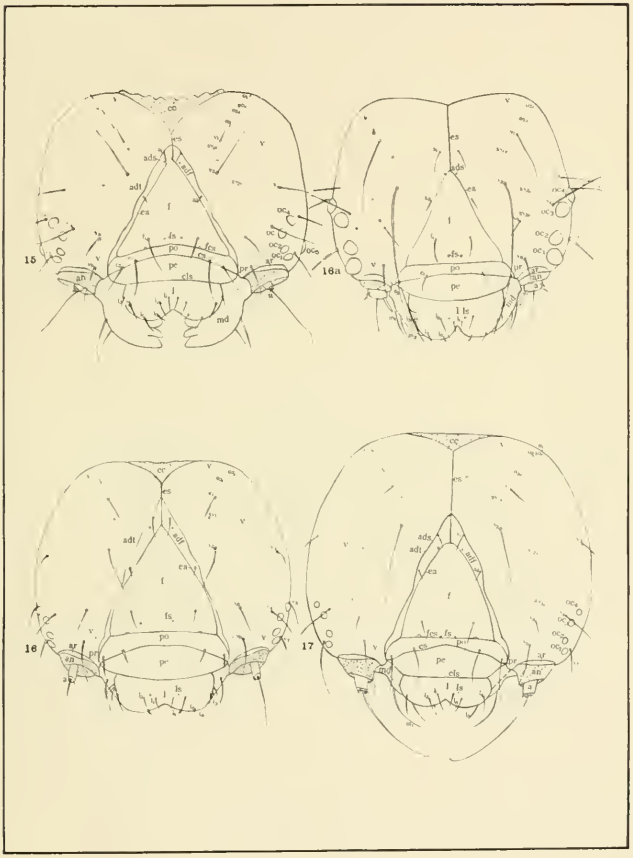
PLATE IV

EXPLANATION OF PLATE IV

CEPHALIC ASPECT OF HEAD

15. *Feltia subgothica*, last instar, cephalic aspect of head.
16. *Polia renigera*, last instar, cephalic aspect of head.
16a. *Polia renigera*, first instar, cephalic aspect of head.
17. *Chloridea armigera*, last instar, cephalic of head.

a antenna
a1–2 adfrontal setae
adf adfrontal sclerite
ads adfrontal sensorium
adt adfrontal suture
an antacoria
ar antennaria
c1–2 clypeal setae
cc cervacoria
cls clypeo-labral suture
cs clypeal suture
ea epicranial arm
es epicranial stem
f front
f1 frontal setae
fcs fronto-clypeal suture
fs frontal sensorium
l labrum
l1–6 labral setae
m1–2 mandibular setae
md mandible
o1–3 occipital setae
oc1-6 ocellarae
pe preclypeus
po postclypeus
pr precoila
sv1–3 vertical sensoria
v vertex
v1-13 vertical setae



RIPLEY NOCTUID LARVAE PLATE IV

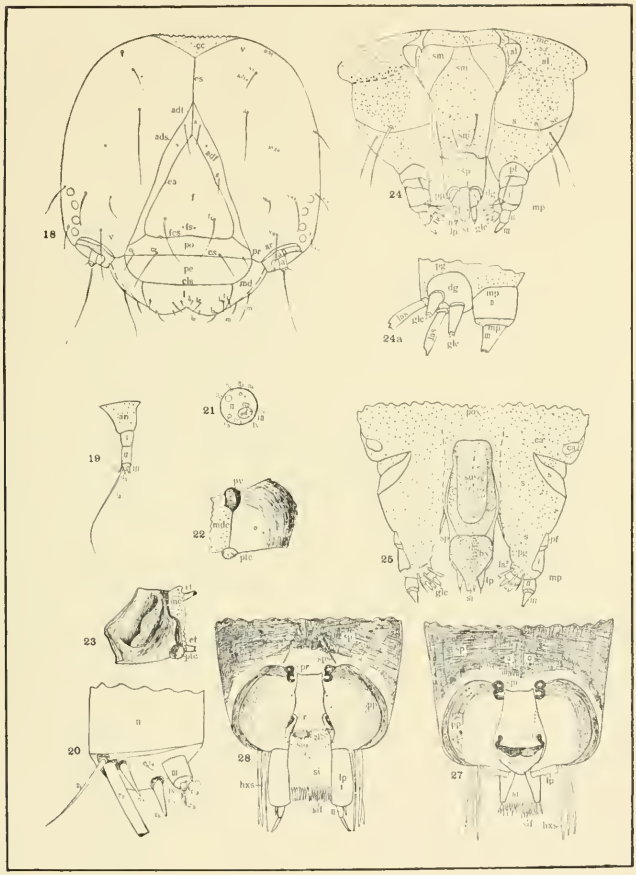
PLATE V

EXPLANATION OF PLATE V

HEAD AND MOUTH-PARTS

18. *Ceramicc picta*, last instar, cephalic aspect of head.
19. *Cirphis unipuncta*, last instar, cephalic aspect of right antenna.
20. *Cirphis unipuncta*, last instar, distal end of antenna.
21. *Cirphis unipuncta*, last instar, diagram of distal end of antenna.
22. *Cirphis unipuncta*, last instar, lateral aspect of right mandible.
23. *Cirphis unipuncta*, last instar, mesal aspect of right antenna.
24. *Cirphis unipuncta*, last instar, caudal aspect of labium and maxillae.
24a. *Cirphis unipuncta*, last instar, distal end of maxilla, caudal aspect.
25. *Cirphis unipuncta*, last instar, hypopharynx and cephalic aspect of labium and maxillae.
26. *Cirphis unipuncta*, last instar, distal portion of labium, caudal aspect.
27. *Cirphis unipuncta*, last instar, distal portion of labium, cephalic aspect.

a antenna
a1-2 adfrontal setae
adf adfrontal sclerite
ads adfrontal sensorium
adt adfrontal suture
al alacardo
an antacoria
ar antennaria
c1-2 clypeal setae
cc cervacoria
cls clypeo-labral suture
cs clypeal suture
dg distagalea
ea epicranial arm
es epicranial stem
et extensotendon
f front
f1 frontal setal
fcs fronto-clypeal suture
fs frontal sensorium
hx hypopharynx
hxs hypopharyngeal setae
l labrum
l1-6 labral setae
la lacinia
lp labial palpus
m1-2 mandibular setae
md mandible
mdc mandacoria
mp maxillary palpus
ol-3 occipital setae
pe preclypeus
pl paracoila
po postclypeus
pp palpiger
pr precoila
ptc postartis
py preartis
rt recto-tendon
s stipes
sa subcardo
se secondary suture
si spinneret
sif fringe of spinneret
sio proximal fold of spinneret
sis proximal sclerite of spinneret
sm submentum
sp stipulae
spr sensoria of palpiger
sps stipular setae
sr sensorium
sv1-3 vertical sensoria
v vertex
v1-13 vertical setae



RIPLEY NOCTUID LARVAE PLATE V

PLATE VI

EXPLANATION OF PLATE VI

LABIUM AND SPINNERET

28. *Ceramica picta*, last instar, distal portion of labium, caudal aspect.
29. *Polia renigera*, first instar, lateral aspect of spinneret.
30. *Polia renigera*, first instar, labial palpus.
31. *Polia renigera*, last instar, distal end of labium, caudal aspect.
32. *Polia renigera*, last instar, lateral aspect of spinneret.
33. *Lycophotia margaritosa*, first instar, distal end of labium, caudal aspect.
34. *Lycophotia margaritosa*, first instar, lateral aspect of spinneret.
35. *Lycophotia margaritosa*, second instar, lateral aspect of spinneret
36. *Lycophotia margaritosa*, second instar, caudal aspect of spinneret.
37. *Lycophotia margaritosa*, third instar, cephalic aspect of spinneret.
38. *Lycophotia margaritosa*, last instar, distal portion of labium, caudal aspect.

hsx hypopharyngeal setae
lp labial palpus
sd silk duct
si spinneret
sif fringe of spinneret
sio proximal fold of spinneret
sir rudimentary fringe of spinneret
sis proximal sclerite of spinneret
siu upper lip of spinneret
siw lower lip of spinneret
sp stipulae
spr sensoria of palpiger
sps stipular setae
sr sensorium
ss secondary sclerite

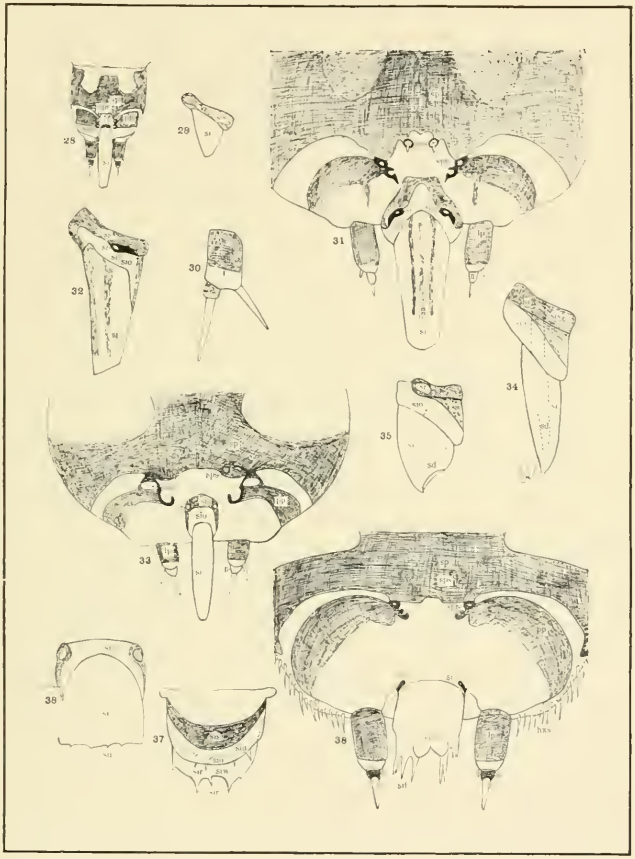

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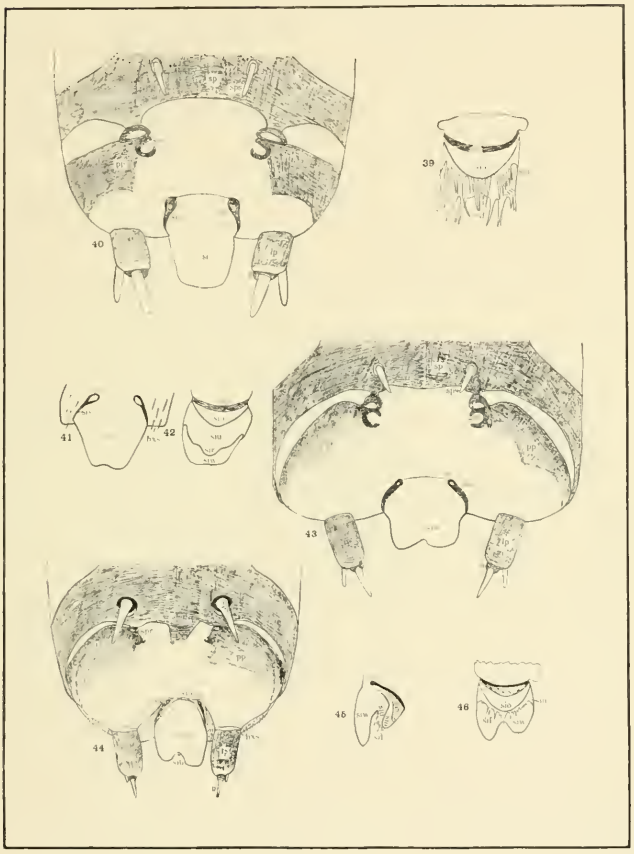
PLATE VII

EXPLANATION OF PLATE VII

SPINNERET

39. *Lycophotia margaritosa*, last instar, cephalic aspect of spinneret.
40. *Agrotis ypsilon*, first instar, distal portion of labium, caudal aspect.
41. *Agrotis ypsilon*, second instar, caudal aspect of spinneret.
42. *Agrotis ypsilon*, second instar, cephalic aspect of spinneret.
43. *Agrotis ypsilon*, third instar, distal portion of labium, caudal aspect.
44. *Agrotis ypsilon*, last instar, distal portion of labium, caudal aspect.
45. *Agrotis ypsilon*, last instar, lateral aspect of spinneret.
46. *Agrotis ypsilon*, last instar, cephalic aspect of spinneret.

hxs hypopharyngeal setae
lp labial palpus
pp palpiger
si spinneret
sif fringe of spinneret
sio proximal fold of spinneret
sir rudimentary fringe of spinneret
sis proximal sclerite of spinneret
siu upper lip of spinneret
siw lower lip of spinneret
sp stipulae
spr sensoria of palpiger
sps stipular setae
sr sensorium



RIPLEY NOCTUID LARVAE PLATE VII

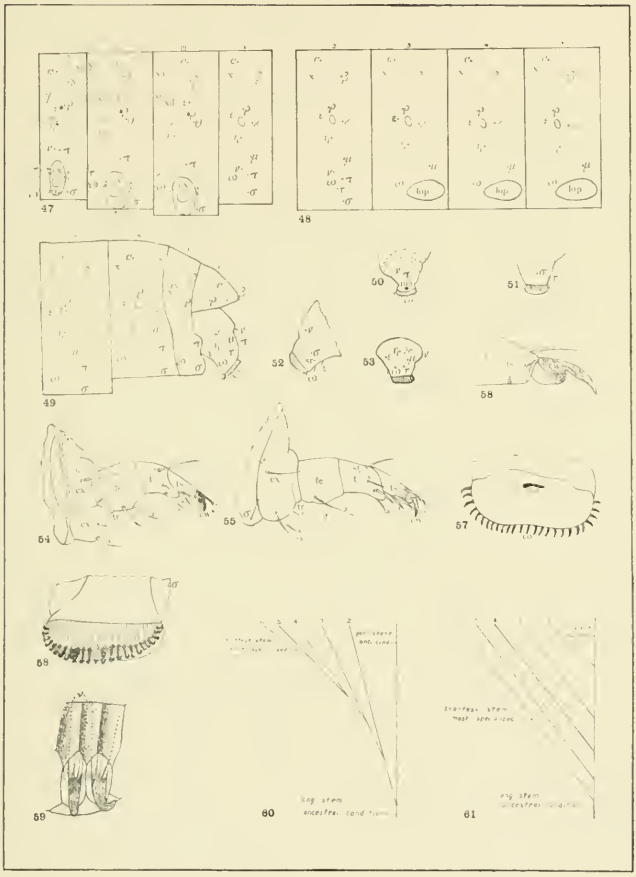
PLATE VIII

EXPLANATION OF PLATE VIII

THORACIC AND ABDOMINAL SETAE, LEGS

47. *Cirphis unipuncta*, last instar, setal maps of thoracic and first abdominal segments.
48. *Cirphis unipuncta*, last instar, setal maps of second, third, fourth, and fifth abdominal segments.
49. *Cirphis unipuncta*, last instar, setal maps of seventh, eighth, ninth, and tenth abdominal segments.
50. *Cirphis unipuncta*, last instar, a median larvapod, lateral aspect.
51. *Cirphis unipuncta*, last instar, a median larvapod, mesal aspect.
52. *Cirphis unipuncta*, last instar, anal larvapod, mesal aspect.
53. *Scolecocampa liburna*, last instar, and larvapod, lateral aspect.
54. *Cirphis unipuncta*, last instar, prothoracic leg, cephalic aspect.
55. *Cirphis unipuncta*, last instar, prothoracic leg, caudal aspect.
56. *Cirphis unipuncta*, last instar, claw of prothoracic leg.
57. *Cirphis unipuncta*, last instar, distal portion of a median larvapod, distal aspect.
58. *Cirphis unipuncta*, last instar, distal portion of a median larvapod, mesal aspect.
59. *Cirphis unipuncta*, last instar, mesal aspect of crochets.
60. Diagram representing the phylogeny of the short epicranial stem as derived from a study confined to the last instar. Erroneous interpretation.
61. Diagram representing the phylogeny of the short epicranial stem as derived from postembryological study. Correct interpretation.

co	crochet	*ma*	muscle attachment
cw	claw	*sr*	sensorium
cx	coxa	*t*	tibia
fe	femur	*ts*	tarsus
lop	larvapod		



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1. The University of Illinois Studies in Language and Literature. Published quarterly. Three dollars a year.

2. The Illinois Biological Monographs. Quarterly. Three dollars a year.

3. The University of Illinois Studies in the Social Sciences. Monographs in history, economics, political science, and sociology. Quarterly. Three dollars a year.

4. The University Studies. A series of monographs on miscellaneous subjects.

5. The Journal of English and Germanic Philology. Quarterly. Three dollars a year.

(For any of the above, address 161 Administration Building, Urbana, Illinois.)

6. The Bulletin of the Engineering Experiment Station. Reports of the research work in the Engineering Experiment Station. Address Director of Engineering Experiment Station, University of Illinois.

7. The Bulletin of the Agricultural Experiment Station. Address Director of Agricultural Experiment Station, University of Illinois.

8. The Bulletin of the State Laboratory of Natural History. Address Director of State Laboratory of Natural History, University of Illinois.

9. The Bulletin of the State Geological Survey. Address Director of State Geological Survey, University of Illinois.

10. The Bulletin of the State Water Survey. Address Director of State Water Survey, University of Illinois.

11. The Report of the State Entomologist. Address State Entomologist, University of Illinois.

12. The Bulletin of the Illinois Association of Teachers of English. Address 301 University Hall, University of Illinois.

13. The Bulletin of the School of Education. Address 203 University Hall, University of Illinois.

14. The Law Bulletin. Address 207 Law Building, University of Illinois.

15. The general series, containing the University catalog and circulars of special departments. Address The Registrar, University of Illinois.

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